

Clément Vigier

Mountain grasslands dynamics: integrating phenotypic plasticity in a new agent-based model



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Présentée par

Clément VIGUIER

Thèse dirigée par **Bjorn REINEKING (CSV)**, IRSTEA

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**Dynamiques des prairies de montagne :
intégration de la plasticité phénotypique
dans un nouveau modèle à base d'agents**

**Mountain grasslands dynamics: integrating
phenotypic plasticity in a new agent-based
model**

Thèse soutenue publiquement le ,
devant le jury composé de :

Monsieur Bjorn REINEKING

DR2, IRSTEA Grenoble, Directeur de thèse

Madame Uta BERGER

Professeur, Technische Universität Dresden, Rapporteur

Madame Marie-Laure NAVAS

Professeur, Montpellier SUPAGRO, Rapporteur

Madame Annabel PORTE

Directeur de Recherche, UMR Biogeo, INRA Université de Bordeaux ,
Examinateur

Monsieur François MUÑOZ

Professeur, LECA Université Grenoble Alpes , Examinateur



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I

INTRODUCTION

1 CONTEXT

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

1.1.1 The value of ecosystems: from properties to services

Everyone has a particular relationship with nature. The representation of the nature depends on the way we experienced it – temperate or tropical forests, mountain rivers or cliffs on the ocean littoral, bird songs or wind between stones. Anyone who shares one of these visions will likely want to preserve natural systems. But facing this emotional perception and inner desire to see these ecosystems preserved, there are other forces that push in opposite directions. All indexes of the biodiversity decrease at dangerous rates (Butchart *et al.*, 2010), despite increasing local efforts and positive effect of conservation fundings (Waldron *et al.*, 2017), the deforestation threatens the largest forest systems, insects are less and less presents (Hallmann *et al.*, 2017) and animals are repelled to fragmented and diminishing habitats (Tucker *et al.*, 2018). 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**² was developed by Costanza *et al.* (1997) to capture the value of **ecosystems**. It encompasses the benefits humans extract from ecosystems. It enables a categorisation of services and their quantification (up to the level of 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 benefits does nature provide us? If one could be tempted to answer that the value of an ecosystem cannot and/or should not be measured, it is clear that all ecosystems do not benefit 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.

² highlighted terms correspond to key terms and are listed in the index at the end of this document.

SERVICES

The term **mountain grasslands** designates, in this document, all grasslands, below and above the treeline³, that have short growing seasons delimited by snow-covered periods and experience high variation in temperature and water availability. This term is intentionally generic as the scope of this work is relatively broad and rather theoretical.

Mountain grasslands provide numerous services that can be divided into multiple categories such as provision, cultural, and regulating services (see fig-

³ where *alpine* almost exclusively refers to above the high altitude treeline (Körner, 2003).

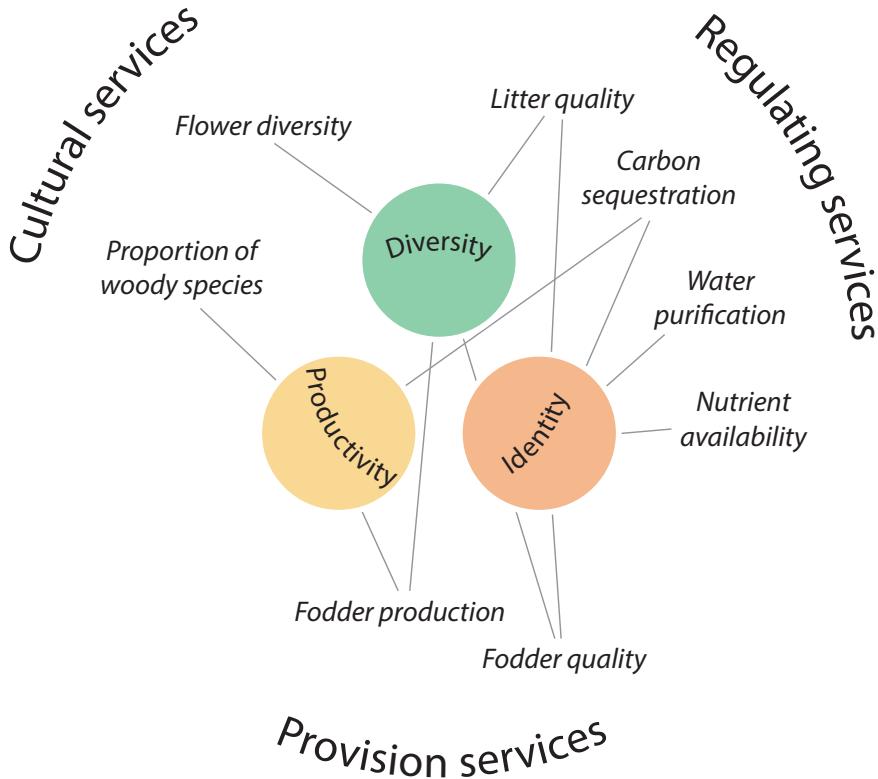


Figure 1.1: Classification of some of the ecosystem services provided by the mountain grasslands, linked to the main properties (circles) of the grassland communities.

ure 1.1). Provision services are related to the quantity and quality of primary resources the grasslands provide. Fodder production and quality are the main measures of provision services. Other services can be included in this category: diversity of flowers and phenology for flower and honey production for instance. Productivity is also relevant to assess carbon capture, a regulating service. Soil nutrient availability and water filtering are other regulating services impacted by the identity and diversity of species populating mountain grasslands. Finally, cultural services, related to tourism activity and landscape appeal are also related to grassland species diversity.

In case of terrestrial ecosystems, vegetation cover is often central because of its role in primary production, and the fact that vegetation community informs about the properties of the abiotic and biotic conditions. Moreover, most of studies on services from terrestrial ecosystem are interested in plants and soil invertebrates Bello *et al.* (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 global change because they cannot escape changes in conditions and are the target of management practices linked to fodder productions. All these arguments support the interest of studying the vegetation dynamics for the assessment of ecosystem services.

Ecosystem services are tightly related to **ecosystem properties** (as illustrated in figures 1.1)(Díaz, Lavorel, Bello, *et al.*, 2007; Lavorel & Garnier, 2002) that can be extracted from a 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 its community's dominant species (or directly its characteristics) that transfers its traits to the whole community. It can also refer to mean traits (with community-weighted mean measures) of a community. In this document, identity will often be used to talk about the resource-use strategy (*i.e.* whether it is more or less exploitative. The term **exploitative** designates species that have rapid growth and lower resource use efficiency.)(Grime, 1977). 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 volume³ 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 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 service levels to plan management practices in the context of global change. Some ecosystem services are linked to the main community properties as illustrated in figure 1.1. Because services are hard to assess, ones can take advantage of this link and assess levels of ecosystems services based on a detailed description of the community; of both its structure and properties. The structure is defined by the relative abundance of the different species of the community, and properties result from the combination of the structure and the specific characteristics of present species. Multiple drivers affect the relative abundance and characteristics of a given species, from abiotic filtering processes to biotic interactions. Thus, ecosystem services also largely depend on abiotic factors (Lavorel & 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 an ecosystem's abiotic and biotic properties. In mountain ecosystems, the plant community is arguably the most dynamic and complex driver of ecosystem services, but direct links can be drawn between a fine description of the community and ecosystem services. Understanding and prediction the main dynamics that capture those links is necessary to efficiently predict changes in levels of ecosystem services.

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.

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

³ volume of the space drawn by the functional traits of interest occupied by living species. It is a simple measure of the functional diversity. See Laliberté & Legendre (2010) for alternative indexes.

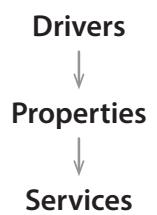


Figure 1.2: Link between abiotic drivers, community properties and ecosystem services.

1.1.2 Global change: what changes and what consequences

Mountain grasslands are maintained by strong climatic constraints that limit growth rate and lifeforms (Körner, 2003), but also by frequent grazing or cutting perturbation regimes that strongly limit the growth of woody species and favour low stature species or rapid growth herbs (Díaz, Lavorel, McIntyre, *et al.*, 2007). But these drivers are changing at alarming rates with negative consequences on levels of ecosystem services (Schröter *et al.*, 2005). Moreover, mountain grasslands are suspected to be very vulnerable (Engler *et al.*, 2011; Schröter *et al.*, 2005) 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 best known and easily observable phenomenon (see figure 1.3). But mountain grasslands will also experience more frequent and severe drought event as well as precipitation events (Beniston *et al.*, 1997; Intergovernmental Panel on Climate Change, 2014; Solomon *et al.*, 2007). Despite being relatively free from non native species, they are also predicted to experience longer growing seasons and stronger invasive pressure from alien species and species from a lower altitude (Alexander, Lembrechts, *et al.*, 2016).

CLIMATE CHANGE

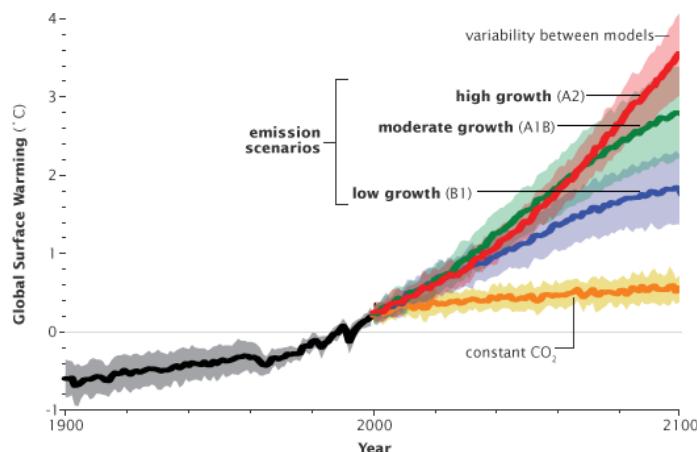


Figure 1.3: Historical models and projection scenarios for global mean temperature from Solomon *et al.* (2007)

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

In addition to changes in climate, land use is also modified. Land-use, mowing or grazing in alpine grasslands, is an important filter for slow-growing perennial species that try to accumulate biomass over multiple seasons. Because of such asymmetric effects, land-use acts as a strong driver and can cause mountain grassland communities to shift in dominant species, and thus along service gradients (Schirpke *et al.*, 2013). Land-use abandonment is suspected to greatly impact the invasion dynamics as it removes the pressure of biomass removal (Carboni *et al.*, 2018).

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, changes of management of mountain grasslands will also affect community dynamics and particularly competition hierarchies. These modifications of strong drivers will have large effects on plant communities, and therefore on the attributes and the services they provide.

Mountain grasslands provide numerous services that can be assessed thanks to main attributes of the plant community. But global change threaten 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 , but most importantly in ways never experienced by living species in recent history(Butchart *et al.*, 2010; Intergovernmental Panel on Climate Change, 2014). 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 considered to not be a good predictor of its current behaviour. The complexity of the prediction goes beyond the multiplicity of dimensions impacted by the global change (rising mean temperature, frequency, and amplitude of drought events, reduction of cutting frequency or grazing abandonment, etc...), as the drivers often interact, with positive or negative feedbacks.

A NEW WORLD

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

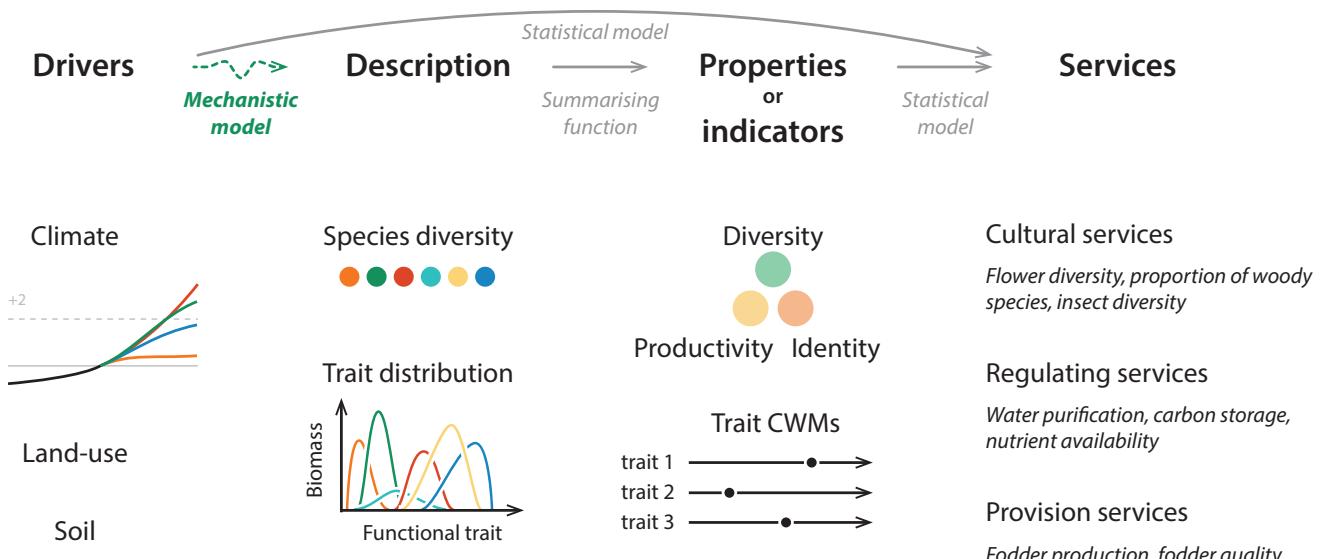
FIND BALANCE

But these common garden or transplant experiments also show contrasting responses, that can come from opposite responses between the intra-specific level and the 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 *et al.* (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 drivers that structure these ecosystems. It may also requires to identify eventual the interactions between those. For such complexity, empirical studies provide required and fundamental knowledge of processes and basic differences between effects, but no consensus can be made (Merilä & Hendry, 2014) and additional approaches need to be developed and used.

An additional argument for the use of alternative approaches is the uncer-

tainty around climate scenarios (see figure 1.3). Indeed, the future of the atmosphere, and by consequence climate, depends mainly on how we humans are capable of changing our dependency on fossil energy (Intergovernmental Panel on Climate Change, 2014). The will to adjust management scenarios to the future of vegetation community (Schirpke *et al.*, 2013) also require extensive experimentation (Deléglise *et al.*, 2015; Martin *et al.*, 2012; Rodriguez *et al.*, 1999).



Mechanistic approaches allow better linking of drivers with community dynamics. This link can then be used to assess levels of ecosystem services as illustrated in figure 1.4(Bello *et al.*, 2010; Lavorel, Grigulis, *et al.*, 2011).

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 & Thuiller (2009) highlight stronger responses to climate change from vegetation communities within niche-based distribution models than within process-based models that capture adaptation mechanisms. More mechanistic processes should be included in these approaches (Evans *et al.*, 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 & Tielbörger, 2015), while it can in other cases shift interactions from competition to facilitation (Callaway *et al.*, 2003).

Phenotypic plasticity adds another level of complexity to the dynamic of communities and the interacting drivers. Statistical or expert based prediction cannot easily 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 by mechanistic approaches to predict the composition and structure of the community. This description can then be used to assess the levels of ecosystem services through statistical models, to evaluate climatic scenarios or alternative land-use practices.

1.2.3 The rise of individual-based approaches

Individual-based-models (IMBs) let the complex behaviours of systems composed 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 hypotheses. Most of these hypotheses deal with the essential resources: light is often ignored in grasslands, while forest models focus on this aspect of resource competition. The choice of model simplifications depends on the focus of the modelling exercise, and the importance of the given variables for the dynamics of the system.

These IMBs of plant communities have been used to investigate the effect of climate change in the study of Rodriguez *et al.* (1999) with the model LINGRA-CC and show an increase in productivity with predicted climate change. But such analysis is not decoupled from the land-use practices, and in this example, the increase in productivity is shown to allow a higher cutting frequency. Alternative scenarios are also explored in other grassland models that take advantage of the mechanistic approach of the model to predict properties of the communities under different conditions or management scenarios (Maire, Gross, *et al.*, 2009; Maire, Soussana, *et al.*, 2013; Taubert, 2014; Taubert *et al.*, 2012). Forest modelling present also numerous implementations of individual-based models based on mechanistic functioning and trade-offs to better understand the drivers structuring diverse communities (see Falster *et al.* (2016) and Maréchaux & 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 used to study patterns of diversity (Boulangeat *et al.*, 2014) or the impact of evolutionary processes on adaptation to climate change (Cotto *et al.*, 2017).

1.2.4 Gaps to fill: plasticity

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

process are explicitly represented (unlike stomatal conductance with stomatal regulation processes) leading to a misrepresentation of these variables (especially root:shoot 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 there is a dichotomy between growth models that are mainly interested in individual processes and species dynamics (Lohier, 2016; Soussana *et al.*, 2012; Taubert, 2014), and models interested in species-level processes and community dynamics (Boulangeat *et al.*, 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 *et al.* (1999), but still with the perspective of productivity). The latter is more interested in larger scale dynamics driven by the climate and evolutionary processes. The questions investigated 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 dynamic global vegetation models (DGVMs¹) despite finer scale interactions. This dichotomy highlights the lack of integrative models that support community dynamics at long time scales with modelling of processes at the individual scale, based on explicit resource dynamics. The explicit modelling of the link between plant strategies, plant functioning, resource dynamics and plant growth allows a solid integration of plant interaction and external drivers (via the effect of resource dynamics and plant growth). Moreover, phenotypic plasticity can be integrated at the plant level, while its complex effects are emergent. Finally, considering the growth of individuals, the strategies of species and the dynamics of the population is required to predict main facets of mountain grasslands communities (diversity, productivity, and identity) that can integrate both management practices and climate scenarios.

Because models have often practicality objectives, it is easier to develop a model that can be calibrated with species-specific empirical data. They can also be calibrated with Bayesian procedures and pattern-based approaches (Hartig *et al.*, 2011). As a consequence, these models often integrate a limited number of species or functional types. This requirement of calibration limits the number of species simulated. To model diverse communities and evolutionary processes, this species diversity is required and a generic framework is an attractive solution to avoid the calibration of individual species. Such high species diversity is observed in DGVMs that integrate trade-offs and multiple strategic axis (Kleidon & Mooney, 2000; Pavlick *et al.*, 2013).

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 environmental conditions and species strategies. Considering both levels is compulsory to capture the complexity of

DICHOTOMY BETWEEN MODELS

¹ model at large scale that regroup plant species into wide functional groups and analyse large-scale dynamics. See Kleidon & Mooney (2000) for an example.

WHERE IS THE DIVERSITY

BUILDING BRIDGES

responses of vegetation communities exposed to diverse drivers.

2 AIMS, OBJECTIVES, AND OVERVIEW

2.1 Aims: understanding and prediction

Global change is probably the biggest challenge humanity has to face at the beginning of this millennium. Actions are urgently needed to reduce the release of carbon dioxide but also to mitigate the effect of climate change on natural and semi-natural systems. While solutions for the former must be found in technology, economics, and sociology, 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 are promising.

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

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

Traditional empirical approaches of observation and controlled experiments provided valuable information on the functioning of grassland ecosystems. However, they lack the power to quantitatively explore the consequences of the intricate interplay of the multiple processes, 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. Disentangling the effects of the different sources of intra-specific variability can help us understand and predict their specific roles in the grassland dynamics. The explicit integration of species-specific phenotypic plasticity in a plant community model can help identify the specific consequences of this process and understand its effects.

As multiple services derive from the main properties of the vegetation of mountain grasslands, it is crucial to establish how phenotypic plasticity specifically impacts these properties. Because these properties depend both on properties of the individuals and the relative abundance and diversity of species, effects on processes at both individual and community scales should 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. Chapters IV and V present respectively individual and community scale results of simulations made with the developed model *MountGrasson* the effects of phenotypic plasticity on main plant community properties. The final chapter discusses the outcomes of this work and possible paths to follow from the presented conclusions. Further model developments are also proposed.

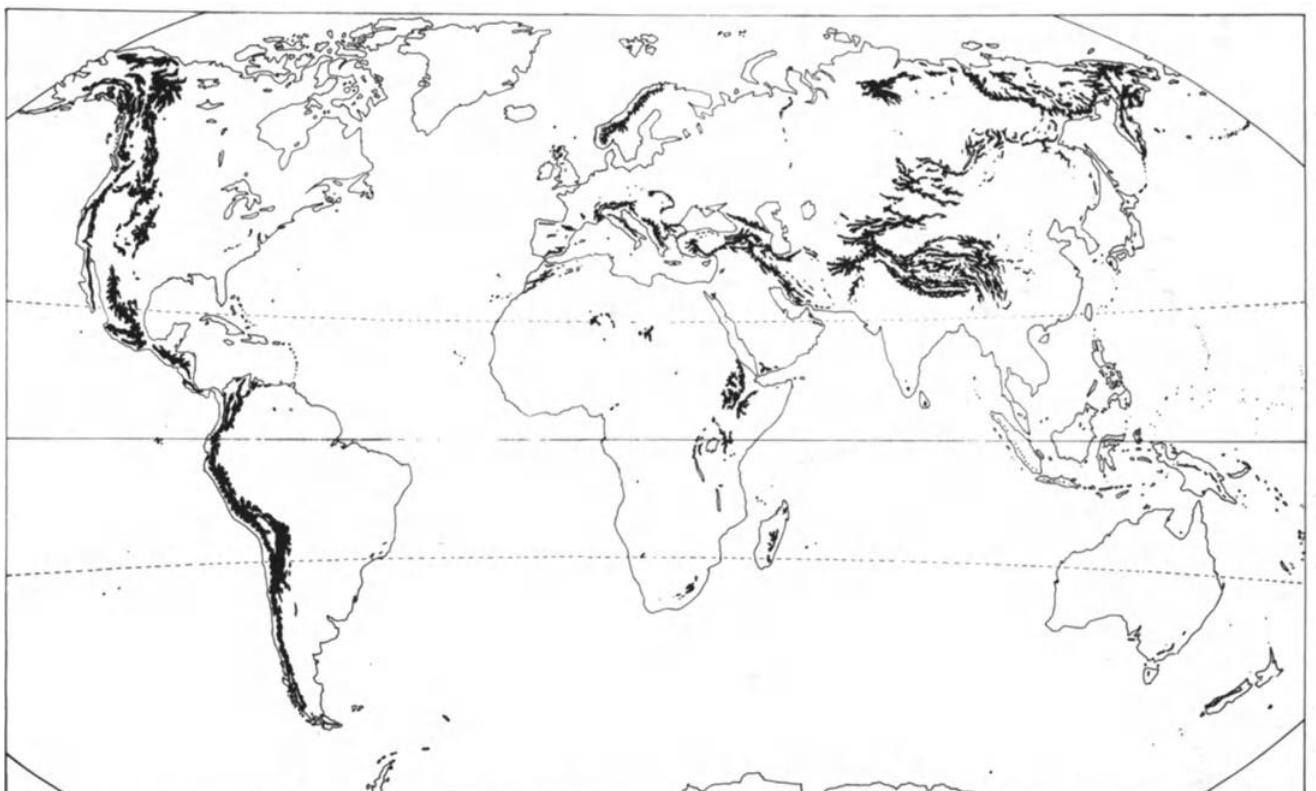


Figure 2.1: Distribution of alpine habitats. Alpine habitats shelter unique and rich ecosystems providing numerous services to human populations. Climate change and mutations of land-use practices threaten these dispersed and fragile habitats. From Körner (2003), reproduced with the permission of Springer, license number: 4384831420904.

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II

BACKGROUND: COMMUNITY DYNAMICS, TRAITS AND PHENOTYPIC PLASTICITY

This chapter aims to introduce the concepts and hypotheses used and interrogated in following chapters and is based on a review of the literature. First, a link between properties of the community and the ecosystem services is 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 investigated.

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 placed on 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 needs 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, the 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 interactions with other species or biotic conditions. The joint effects of the abiotic and biotic environment are captured by the concept of the niche (Elton, 1971). While there are many concepts around the niche, 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 constrain 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 plant development. Other abiotic factors can be considered, such as salinity (L. Poorter & Bongers, 2006) or soil properties (pH). These variables determine if a plant (depending on its specific properties) can establish in 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 abiotic factors are considered is called the **fundamental 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 (as defined by the fundamental 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 2 in figure 1.1). Competition interactions are major factors shaping vegetation community and are extensively studied both with theoretical (Amarasekare, 2003; Chesson, 2000a) and empirical approaches (Kunstler *et al.*, 2016).

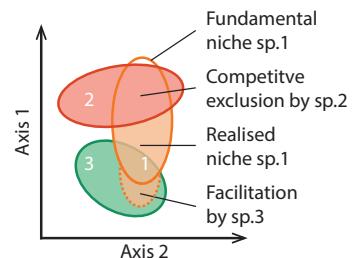
BIOTIC FILTERING

Figure 1.1: The fundamental 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 IBMs.

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, *et al.*, 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 a matrix, in addition to being hard to parametrise, cannot be used in a framework of dynamic strategies as the changing traits would change the interaction¹. 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 (Berger *et al.*, 2008; Morin & Thuiller, 2009).

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 a given species' distribution. While a traditional view of the niche requires considering both abiotic filters and pairwise biotic interactions, fundamental niches and resource dynamics modelling offer an alternative to model realised niches as an emergent property of the model.

1.1.2 The complexity of coexistence

If one wants to better understand and predict dynamics of complex systems, one first needs to understand how such complexity 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 (Chesson, 2000b; Levine & HilleRisLambers, 2009).

To predict the outcome of competitive 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 grows better than 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, HilleRisLambers & Levine (2007) in the modern coexistence theory. It states that niche differences (Levine & HilleRisLambers, 2009) and fitness differences are the two mains axes 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

¹ A trait-based interaction matrix could be used, but the benefit of the mechanistic approach would be reduced.

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, the larger are the chances of coexistence. The importance of niche differences required for stable coexistence decreases with the decrease in fitness differences.

On the other hand, Tilman elaborates a theory (D. Tilman, 1982, 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. Co-existence is possible if there is more than one limiting resource. In this case, co-existence can be achieved if species have a stronger impact on the resource from which they benefit the most (and intersecting zero net growth isoclines).

These two theories give strong conditions for stable co-existence, 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 *et al.* (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 situations to be applicable in the context of diverse mountain grasslands.

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

1.1.3 Variability and dynamics: driven by the resource

Resource dynamics, even with constant resource influx, seems to be the key to understanding plant interactions and dynamics according to D. Tilman (1988). Can the resource distribution in time and space explain co-existence?

In Tilman's perspective, resources are driven by two things, external influx and internal (to the system) consumption or cycling. The system's structure and composition are 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 gap models. Mature forests produce big trees that fall down and create perturbation within the system. The resulting opening in the canopy enables 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 co-existence at a large scale, a co-existence that can be captured by spatially explicit models (Chave, 1999; Falster *et al.*, 2016).

COMMUNITY DYNAMICS

Such drastic dynamics do not exist in mountain grassland 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 a given species cannot be the most competitive species for all conditions in the whole range of conditions experienced in mountain habitats, there is a succession of species at the top of competition hierarchy (Adler, HilleRisLambers, Kyriakidis, *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.

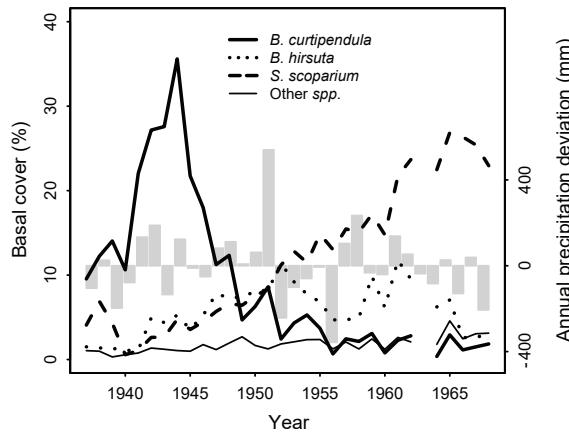


Figure 1.3: Changes in observed basal cover for 3 grassland species. This variation in hierarchy illustrates the succession in grassland communities and the storage effect due to the stabilizing effect of climatic variation promoting coexistence. See details in original study by Adler, HilleRisLambers, Kyriakidis, *et al.* (2006), reproduced with permission of PNAS, Copyright (2006) National Academy of Sciences.

This mechanism promoting coexistence because of succession dominance driven by temporal changes in environmental condition is called storage effect (Adler, HilleRisLambers, Kyriakidis, *et al.*, 2006). 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 (G. D. Tilman, 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 opportunities 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 they are connected by dispersal vectors such as wind and animals. These connections support diversity but not stable coexistence, but remain crucial for

TEMPORAL HETEROGENEITY

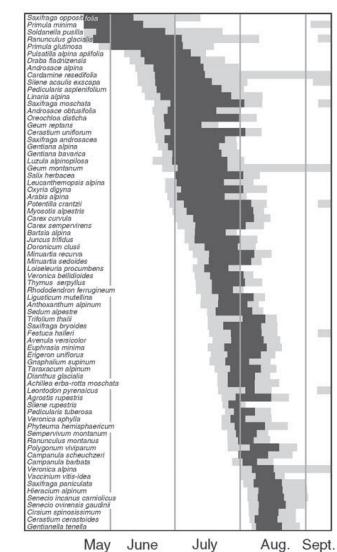


Figure 1.2: Diversity of flowering periods of alpine species. Evidence of succession in grassland ecosystems. From Körner (2003), reproduced with the permission of Springer, license number: 4384850014523.

SPATIAL HETEROGENEITY

LARGER SCALE DYNAMICS

community dynamics. Indeed, the link between the community and the meta-community (all connected communities) is a source for a species that may be absent from the focal community (Alexander *et al.*, 2016). Therefore, in case of transition of environmental 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, but constitutes a driving mechanism of community dynamics and a source of species coexistence. Therefore, it is interesting to try to create such levels of diversity *in silico* with a higher level of processes as found in theoretical models.

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 alone 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. This level of complexity complements the theoretical models and should allow to test the robustness of processes described by these models. However, modelling both community properties and resource dynamics require an understanding of plant functioning and diverse growth strategies. The challenge of community modelling is to keep simplicity in the structure, to integrate the main driving processes and to enable the representation of multiple strategies related to these 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? 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.

A challenge of modern community ecology is to determine the trajectories 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 fully tackle this problem. While the focus shifts toward community approaches, modelling tools should evolve to better answer these newly investigated questions. 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 presence 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. Despite the growing availability of the type of data required to such models, their design does not match the questions relative to transitory dynamics. 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. Considering these processes allows to explicit and decompose plant functioning, and therefore could improve the representation of this functioning under new combinations of environmental conditions.

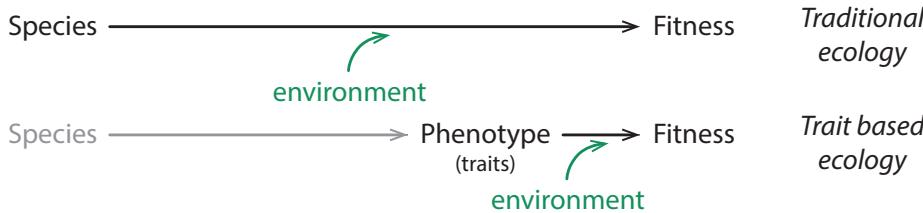


Figure 2.1: The shift toward trait-based ecology allows for the decomposition of the link between species and fitness determined by the environment. On one hand, the link between species and traits is better characterised by standardised protocols and the use of databases such as Kattge *et al.* (2011). 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 (Reich, Walters, *et al.*, 1992), and then link species to traits with simpler data collection procedure (Cornelissen *et al.*, 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. The singularity of the species is exchanged for a 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 & Reich, 1999; L. Poorter & Bongers, 2006; 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 *et al.*, 2003) allowing pooling of the data into big databases such as TRY (Kattge *et al.*, 2011) or Glopnet (Wright, Reich, *et al.*, 2004). 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.

The use of large data sets unlocks the study of large scale patterns that could be studied before in ecology. For example, Niinemets (2001) show strong global patterns along climatic variables for shrubs and trees all over the planet. The mean monthly precipitation of the three driest month and the incident daily mean global solar radiation are correlated to leaf structural traits. Such patterns are also observed for leaf structural and chemical traits in Wright, Reich, *et al.* (2004).

But the functional traits can be used at a more local scale to disentangle the species and the community responses (Jung, Albert, *et al.*, 2014; Kichenin *et al.*, 2013).

The species-centred ecology has limitations to fully capture the complexity of coexistence and community dynamics processes. The last two decades saw the rise of functional ecology and its ability to capture quantitatively relationships between vegetation and abiotic gradients. The capacity to generalise ecological patterns thanks to easily measurable traits open the door for generalised theories on plant functioning.

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 tempting 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 *et al.*, 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 *et al.* (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, Riibak, Tamme, *et al.*, 2016). Due to their complexity, interactions cannot be summarised by single trait value comparison but is multi-dimensional (Kraft *et al.*, 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 environmental 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 effects 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 assemblages. Understanding this structure and how it relates to community dynamics and external drivers is crucial for the representation of diverse communities under changing environments.

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 (Chave *et al.*, 2009; Reich, Wright, *et al.*, 2003; Reich, 2014; Wright, Reich, *et al.*, 2004) and within species (Hu *et al.*, 2015). This correlation between functional traits of the leaf was described at a global scale by Wright, 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 process 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 a large fraction (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 axis (Díaz *et al.*, 2016).

Similar correlations could be found in roots (Reich, 2014; Ryser, 1996) 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 (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 re-

LEAF ECONOMIC SPECTRUM

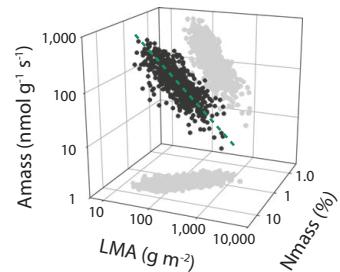
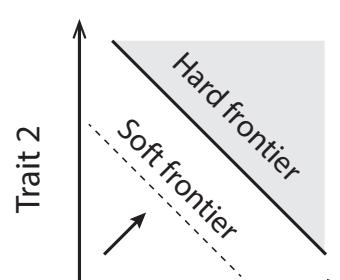


Figure 2.2: Three dimensions of the LES. Correlation of Leaf Mass Area, assimilation rate per mass unit and nitrogen concentration. This correlation reduces three dimensions (more dimensions not shown) into one axis (—). From Wright, Reich, *et al.* (2004), reproduced with the permission of Springer, license number: 4384850435840.

STRATEGIES

EMERGENCE



lationship 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 2.3) on one side of the relationship, while competition processes out-select combinations of traits that are not relevant on the other side ("hard frontier" in figure 2.3).

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 characterisations of these constraints should allow a better representation of plant functional diversity.

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 a multiplicity of strategies. In an early attempt to make sense of this diversity of strategies, Grime (1977) theorises the existence of two types 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) highlighted the difficulty to use such space and its incapacity to explain some patterns. According to Westoby, a strategy space² should:

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

Westoby 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

FROM THEORY TO TRAITS

¹ regions of both high stress and high perturbation do not allow establishment

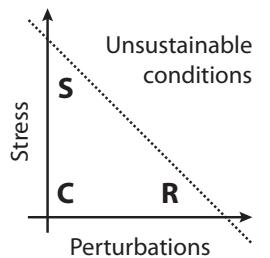


Figure 2.4: Grime's triangle. Competitive (C), stress tolerant (S), and ruderal (R) strategies are dominant in the three regions of the perturbations-stress space.

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

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 also captures ruderal axis (time interval between perturbations)
- Seed mass (S): expresses the capacity of a species to invade recently 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 comparisons between species around the globe (Pierce *et al.*, 2013).

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, 2014). 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 2.3 and Shipley *et al.* (2006)). Therefore, for a given pair 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 trade-offs appear thanks to filtering processes that push the 'soft frontier' toward the 'hard biological frontier' (in figure 2.3), and resource exchanges in relation with resource availability are such processes. 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 (Körner, 2003). Resource use strategies and reproductive strategies are also orthogonal (Díaz *et al.*, 2016). From this, a generic principle can be formulated stating that the number of observable trade-offs in an ecosystem is close to the number of constraining processes. It is supported by the observation that a limited number of traits (or dimensions, or trade-offs) is often enough to capture the diversity of a vegetation community as in Laughlin (2014).

The independence of strategic trade-offs justifies that the use of these trade-offs 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 (Díaz *et al.*, 2016; Pierce *et al.*, 2013) 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).

GENERALISATION OF STRATEGY SPACES

EMPIRICAL EVIDENCE

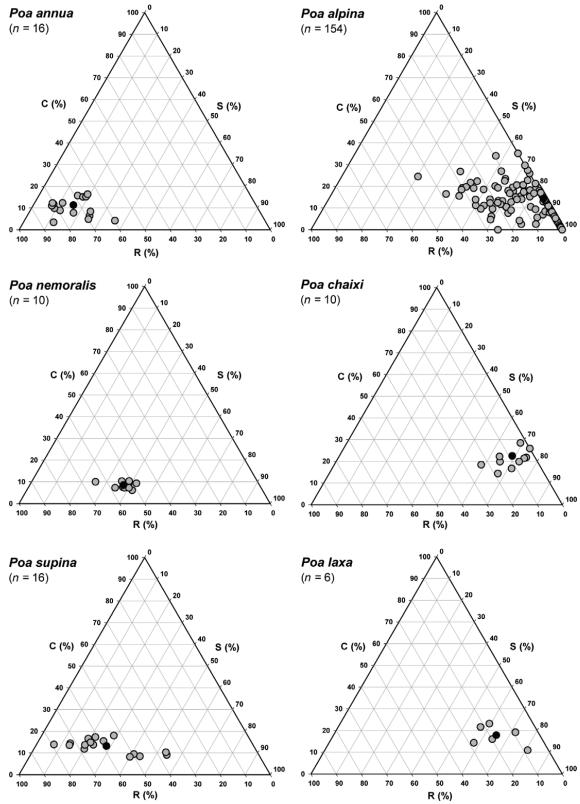


Figure 2.5: Empirical evidence of the CSR triangle in natural communities. The CSR triangle is created by the translation of a multivariate analysis into a coordinate system (see Pierce *et al.* (2013) SI for details). "CSR classification of six species of the genus *Poa* from lowland (left column; *P. 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), reproduced with the permission of John Wiley and Sons, license number: 4384950345235.

The diversity in plant strategies is shaped by the multiplicity of the filtering processes. 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 sets allows easy characterisation of species and communities.

2.3 How traits link to ecosystem properties

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

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

As discussed earlier (chapter I), plant species provide ecosystem services (Mokany *et al.*, 2008). Some of these services are direct consequences of the characteristics 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 often continuous quantitative variables, they can be manipulated more easily than categorical variables. Therefore, while phytosociology describes vegetation communities with broad types and approxi-

mate 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 corresponds to an extended quantitative 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 & 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 diversity, such as the evenness, the spatial scale, the functional dimension (see Chalmandrier (2015) for more 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.

A 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 ecosystem resilience (Mori *et al.*, 2013) and resistance to invasion (Bennett, Riibak, Kook, *et al.*, 2016).

Species richness and functional diversity are often strongly correlated, but

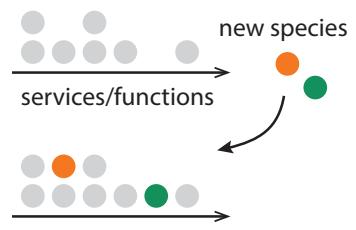


Figure 2.6: Insurance and selection effects. New species increasing diversity either reinforcing existing function (●), or provide new function (•)

they do not capture the same services or effect. Functional diversity is a strong indicator of niche complementarity and its benefits.

2.3.3 Productivity: both community property and ecosystem service

Productivity of a plant community is mostly sensitive to abiotic conditions, precipitation, nitrogen, and temperature being the main variables influencing productivity. Because of this, 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 among the most telling ones.

[]

Table 2.1: A comparison of net biomass production (above- plus belowground) in major types of global vegetation, calculated either per year or re-calculated per month of growing season (approximate ranges in brackets). From Körner (2003).

Table 2.2: table:productivity

Biome	Annual net primary production (kgm ⁻² a ⁻¹)	Length of growing season (month)
Humid tropical forest	2.5 (1.8-3.0)	12
Temperate deciduous forest	1.2 (1.0-1.5)	5
Boreal forest	1.1 (0.3-2.0)	5
Tropical grassland	2.5 (0.2-4.0)	10
Temperate grassland	1.0 (0.2-1.5)	6
Alpine vegetation of the northern temperate zone	0.4 (0.2-0.6)	2

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

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, wood production in forests, etc...

Productivity is at the same time a property of the habitat, and the community, and it is 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 a statistical framework (Lavorel & Grigulis, 2012). 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

capture these trade-offs between services bundles (Lamarque *et al.*, 2014). This link should encourage ecologists 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 could profitably focus on the dynamics of grasslands communities and the changes in main properties.

2.4 Modelling diverse plant communities

Modelling mainly consist in deciding what is important considering and worth representing. The choice of how an entity or a mechanism is represented is also part of this decision making. While considering a vegetation community the choice can be on the resources needed, the type of perturbations, or the part of the life cycle you project to be of most importance. For vegetation models that aim for a 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 spaces open vegetation modelling

In a mechanistic model with multiple species, strategy-spaces are simplified ways to define multiple species. A 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 about 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 spaces based on trade-offs enable the representation of multiple species, in a constrained and closed trait-space. 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. A prime exemple of these models

THE POSITION MAKES THE SPECIES

IN DGVMs

is that of Kleidon & Mooney (2000), and extensions (Pavlick *et al.*, 2013; Reu *et al.*, 2011). 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 environments (Kooyers, 2015). These models (Pavlick *et al.*, 2013; Reu *et al.*, 2011) demonstrate the ability to capture diversity and climatic response patterns, better than plant functional types, with a limited number of traits.

Such approaches are also used to study more specific mechanisms like fire perturbations (Scheiter, Langan, *et al.*, 2013). In this case, specific traits such as investment in bark and wood density, are included. The adaptive value of the traits is modelled 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, but rather focuses on evolutionary dynamics.

Individual-Based Models are great tools to model community dynamics incorporating local interactions and small-scale dynamics. Because they are interested in smaller systems, IBMs often do not use strategy-spaces and prefer species-specific parametrisation (Lohier, 2016; Soussana *et al.*, 2012; Taubert, 2014). This is often explained by the focus on heavily managed grasslands with objectives of productivity that need precise predictions and model a limited number of species. But strategy spaces have been 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.

IN IBMs

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 errors 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

The term **model** represents a large class of simplified representations of real systems, or conceptual ideas. These are always tools to better understand our world, it can be more by their design and their construction or more by their use (simulations). Here the focus is on simulation models, and particularly agent-based models (of grassland systems). How can these models inform us about real systems?

One way models can help us understand a system are simulation experiments. This approach is very similar to empirical experiments. The experimenter puts the system, here the model, in different conditions and confronts the results with hypothetical results predicted by theory being tested. In this case, the model is treated as a functional representation of the reality providing the necessary

HYPOTHESIS TESTING

properties to test the hypothesis. And the model shines here in contrast with the real system by its capacity to test a large number of conditions at very low cost, both in money and time. This is for example the case of the model developed by Taubert (2014) to test the richness-productivity hypothesis. In the model developed by Droz & Pekalski (2013), the mechanistic properties of the model allow to test the link between the type of interactions and the environmental conditions. These simulation models also allow the prediction/exploration of the system behaviour under alternative climate scenarios (Rodriguez *et al.*, 1999; Scheiter & Higgins, 2009). This is particularly interesting when exploring global change scenarios.

But, this requires a certain level of confidence in the model. This confidence is acquired during the building and calibration process, that both can also give insights on the modelled systems.

One model, as it is a simplification of a given system, has often a particular perspective, driven by the questions the scientist tries to answer. Because of that, the modeller tries to reproduce only a fraction of the properties/behaviours of the real system. In this case, the models inform us by their capacity to reproduce these essential properties with a minimum number of features and the minimal complexity. This is helpful to identify and understand the core mechanisms that allow the emergence of a particular behaviour of the system. Reineking *et al.* (2006) show the capacity of simple allocation trade-offs to let emerge species rich communities, in addition to show the importance of the water (temporal and spatial distribution) as a driver of community structure. The complexity of the studied systems or organism often limits the identification of the causes of a given pattern. Models are valuable when they have the capacity to reproduce these patterns with a minimal complexity, identifying the necessary and sufficient components required for the behaviour to emerge. An example here is the work of Lohier *et al.* (2014) on the ontogenetic shift in Root:Shoot ratio for different species.

The calibration process can be necessary to gain confidence in the model, but it also provides new insights. In particular, calibration techniques use data to inform on the value of the model's parameters. These specific parameters can have a value to understand the biology or specificity of the species relatively to other species or the mean behaviour of the model.

A mix of these two forms of insights come from the unique feature of simulation models: their capacity to turn on or off the constituent mechanisms, or rather to switch between different representations of the system. This capacity offers a great flexibility and allows to understand the role of different compartments of the model, and the empirical support for alternative mechanisms. This particular method was used for example in the work of Maire *et al.* (2013) to explore the effects of plasticity on grassland communities.

The use of strategy spaces in models allows the representation of high diversity in a common plant functioning framework, requiring only a limited number of parameters. Such approaches are very useful to follow the dynamics of communities in a mechanistic framework. Fine-scales IBMs 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

MINIMAL REPRODUCTION

ON/OFF BUTTONS

diverse communities at small scales while keeping biological mechanisms at their core. These models can then be used in different ways to build a better understanding of the modelled systems. However, existing model, based on strategy spaces tend to consider mean individuals and ignore individual variations.

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

3.1 Intra-specific variability change the rules

3.1.1 Increasing interest in intra-specific variations

Trait approaches 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 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. Consequently the high functional variability within species would weaken theories and generalisation based on mean traits. Violette *et al.* (2012) suggested that the extent of within-population variability relatively to within-community variability should be considered to avoid mistakes in the estimation of coexistence mechanisms. Ignoring intra-specific variability lead to an underestimation of niche overlap, plastic response to neighbours, or the fraction of resource a species can use. Multiple studies focused on the extent of functional intra-specific variability (Albert, Thuiller, Yoccoz, Douzet, *et al.*, 2010; Albert, Thuiller, Yoccoz, Soudant, *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. 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 increasing community diversity. They also show that the strategic differentiation between exploitative and conservative species is robust to these variations. It appears that not all traits are 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 (Albert, Bello, *et al.*, 2012; Bello *et al.*, 2011). All indexes are not sensitive to the same degree, with single trait measure being the most sensitive, but should be used carefully to interpret ecological pattern linked to functional diversity.

To overcome this difficulty and disentangle the effects of the different forms of functional diversity, specific indexes have been 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 whether variability is structured along environmental gradients, suggesting adaptation mechanisms.

Along such environmental gradients, trait variability for traits like SLA (H. Poorter, Niinemets, *et al.*, 2009) or leaf mass fraction (LMF) (H. Poorter, Niklas, *et al.*, 2012) follow similar patterns as inter-specific response (Niinemets, 2001), with increasing SLA along precipitation and temperature gradients, and decreasing SLA along radiance gradients (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 Albert, Thuiller, Yoccoz, Soudant, *et al.* (2010) for more details). Kichenin *et al.* (2013) argue this 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 (Albert, Thuiller, Yoccoz, Soudant, *et al.*, 2010; Jung, Albert, *et al.*, 2014; Kichenin *et al.*, 2013) leading to difficulties in predicting the response of the community. These levels need to be disentangled, and in order to do that, mechanisms underlying intra-specific variability have to 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; Violette *et al.*, 2012).

After the emergence of trait-based ecology and its high potential, the recent 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 the ways intra-specific variations affect community properties or coexistence mechanisms, but represent a few contrasting examples to emphasise the need for better identification and understanding of underlying mechanisms.

Hart *et al.* (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. This certainly can apply to genetic variations. However, intra-specific variability, such as plasticitic responses and local genetic selection, emerges if there are changes

JENSEN INEQUALITY

or heterogeneity in conditions. These changes, of both traits and environmental conditions, are susceptible to greatly affect the competitive interactions. This conflicts with the assumption of fixed interactions coefficients of such models.

The Jensen's inequality is one of the many mechanism through which the intra-specific variability can impact the dynamics of communities (Bolnick *et al.*, 2011).

Intra-specific variations (ISVs) can also greatly affect the niche, as any new phenotype is likely to be better adapted to an alternative environment. Therefore, this variability widen the potential niche of the species. In addition to have a potential large impact on the community structure and dynamics, the comparison of the different levels of variance give insights on the driving forces shaping the communities (Violle *et al.*, 2012). NICHE

The flexibility offered by a wider niche also impact the mechanisms shaping the community and the relative importance of the habitat filtering and niche differentiation (Jung, Violle, *et al.*, 2010), with potential positive impact on the species diversity.

The previous paragraphs illustrate the contrasted effects the intra-specific variability can have on a community, especially its diversity. Numerous other studies highlight the potential for positive and negative impacts of the intra-specific variability. In addition to already mentioned studies, the work by Courbaud *et al.* (2010) highlight that "intra-specific variability allows flexible patterns of community dynamics and could explain discrepancies between observations and classical theories.". More specific work on the phenotypic plasticity, a specific case of ISV, strong effect of this source of variability. It can lead to a shift from competitive interaction to facilitation interactions (Callaway, Pennings, *et al.*, 2003), or, by impacting the niches, affect negatively the niche separation while at the same time supporting stronger niche differentiation (Roscher *et al.*, 2015). The difficulty to understand and predict the effect of this plasticity is highlighted in the context of the modern theory by the study of Turcotte & Levine (2016). CONTRASTING EFFECTS

Facing this ensemble of contrasted, sometimes conflicting, results, many suggest and support that more work is required to better understand the effect of this variability of the community dynamics (Bolnick *et al.*, 2011; Valladares *et al.*, 2015; Violle *et al.*, 2012), but also try to determine when it should be considered (Albert, Grassein, *et al.*, 2011).

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 their potential effects on the dynamics and properties of the communities, and ecosystems.

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

Before the increasing interest in ISV during the last decade, this variability was treated as a random effect, partly explaining why it was ignored. But, without WHERE IS IT FROM?

discussing too much the philosophy of what is random, we could agree that often the random character of an event is attached to the level of knowledge we have of the conditions leading to this event. That means that intra-specific variability is considered random because we do not have enough information (either too complex, unreachable, or both) do understand/predict the distribution of the different outcomes. But ignoring the mechanisms that lead to this variability causes two simplifications that can alter our interpretations and our understanding of its effects.

First, because it is considered random, ones can overlook the available information about this random event, *i.e.* its distribution. But simply ignoring it, or just apply the same normal normal distribution to all levels of variability. New modelling approaches tend to consider a more precise description of the ISV distribution by looking at its different moments (DeWitt, 2016)(see also Barabás & D'Andrea (2016), to a certain degree). This can lead to errors due to non linearity (Bolnick *et al.*, 2011; Hart *et al.*, 2016), or non perceived continuous behaviours (Courbaud *et al.*, 2010).

Second, considering this variability as random, makes you ignore the underlying mechanisms and therefore implicitly formulate a strong hypothesis on the absence of driving mechanism. This can have strong effect on how ones can interpret fundamental theories (Turcotte & Levine, 2016). This is somehow similar to the default hypothesis of the competition linked to the distance in the trait-space, that ignore hierarchical competition (Kunstler *et al.*, 2016) or non transitivity (Levine, Bascompte, *et al.*, 2017). But establishing coherent hypothesis that explain this variability may not be that easy, and is often biased by a "bell-shape" view of the "random" phenomenons leading to hypothesis that may not explain empirical observations (see the discusion in Kichenin *et al.* (2013) around the hypothesis developed in Albert, Thuiller, Yoccoz, Soudant, *et al.* (2010)).

Considering the underlying process of a phenotypic variability is crucial. This is particularly the case for theoretical models that study the coexistence. In such studies, the conditions are often homogeneous, and therefore the fitness or interactions are solely depending on the traits for the given mean conditions. However, under the hypothesis that the variability has an evolutionary value, some sort of variability in conditions is required to see the emergence of phenotypic variability. Either the phenotypes are stable within individuals but diverse for a given species, and this genetic variability provide gain at the level of the population dynamic. Or if the individuals can adapt to contrasted conditions, and the heterogeneity in conditions explain the variability. In any case, the alternative phenotypes have a better fitness than the phenotype of reference, otherwise these forms of intra-specific variability would have been excluded. Therefore, it suggests that the rules of interaction analysed in these models for the "mean" conditions are not maintained (in term of sign or amplitude) for the specific conditions of the alternative phenotypes.

WHY CHANGING?

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 emergence of new statistical and 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 *et al.*, 2016; Nicotra, Segal, *et al.*, 2015; Zhang *et al.*, 2013) 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 *et al.*, 2014), and a large fraction of the variability observed in grasslands species is a plastic response rather than genetic variation alone (Frei *et al.*, 2014; Merilä & Hendry, 2014).

Nicotra, Atkin, *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.

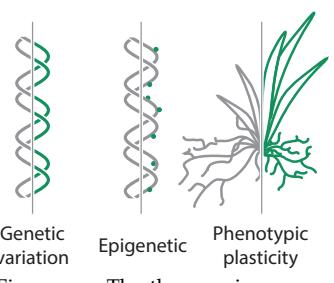


Figure 3.1: The three main sources of intra-specific phenotypic variability: genetic, epigenetic and phenotypic plasticity. Phenotypic plasticity can involve epigenetic mechanisms.

3.2.2 What is phenotypic plasticity?

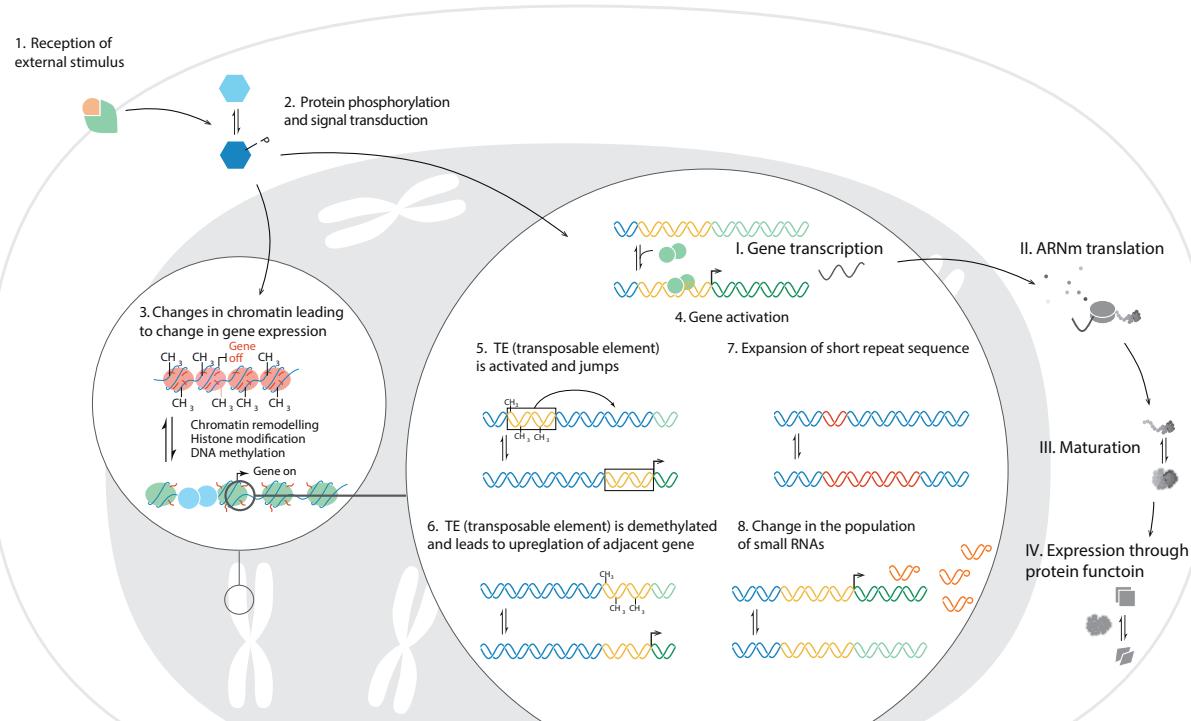
Plasticity is a source of intra-specific variability, but biological processes leading to changes in phenotype can be complex. These paragraphs try to disentangle the different forms of plasticity and the underlying mechanisms.

Box 1: Molecular basis of phenotypic plasticity

The phenotypic plasticity lies both in the perception of external conditions through sensor organ and signalling pathways (auxin pathway for light, root stones 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, question partly explore in this work, but ultimately is applied at the cell levels.

Because of the complexity of these pathways 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.

The processes of information gathering (through specific organs, cells of organelles) and integration of this information finally leading to changes in the phenotype visible at the macro-scale result from similar events at the cell scale. The external signal is captured by a specific receptor at the cell membrane (1), then integrated through phosphorylation cascade (2) leading to numerous alterations of the gene expression sequence (I to IV) because of regulation mechanisms (3 to 8). These regulation mechanisms are diverse, from chromatin changes (3) modifying the accessibility of certain genes, to other gene regulation processes (5 & 6) or post-transcription regulations (7 & 8).



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.

These regulations of gene expression affect the plant behaviour and development. These regulations are reversible (their effect may not be reversible) but can also be inheritable (*i.e.* 6). The type of regulation depends on the targeted genes, the duration of the regulation, and other factors. This multiplicity of regulatory processes at the scale of cells, in addition to the interconnectivity of genes, signalling pathways and tissues interactions, demonstrate an extraordinary potential for the regulation of both functioning and phenotype of plants. Therefore it seems that the molecular basis does not limit the plasticity, but it is rather the difficulty to anticipate the future and to define the best strategies that limits the benefits of phenotypic plasticity.

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 objective ¹ 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

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.

FORMS OF PLASTICITY

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

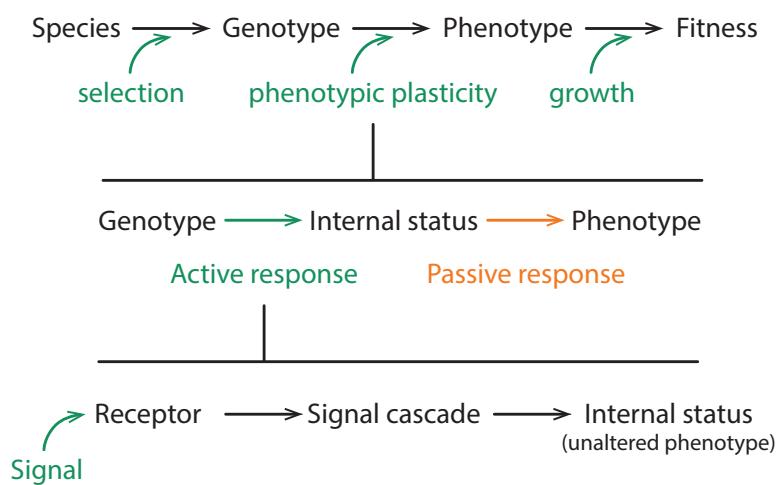


Figure 3.2: Decomposition of phenotypic plasticity as a step between the genotype and the fitness. Phenotypic plasticity is the effect of environment on the link between genotype and phenotype. Plasticity can itself be decomposed in active plastic response that change the internal status of the individual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

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 integrated (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 changes complex development processes. These processes involve numerous proteins and signaling 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 1 above in relationship with gene expression pathway (see also Nicotra, Atkin, *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 conditions. But most of this plasticity is passive, and it could be encompassed in this personal definition of the notion of **growth function** (see figure 3.4). However, among vegetation models only some of them claim to include phenotypic plasticity (Maire *et al.*, 2013). 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 order to have a better fitness is active plasticity see Forsman (2014) for a discussion of the form of 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 *et al.* (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 (middle column). I argue that plasticity, to be considered as an active process, should be under a ge-

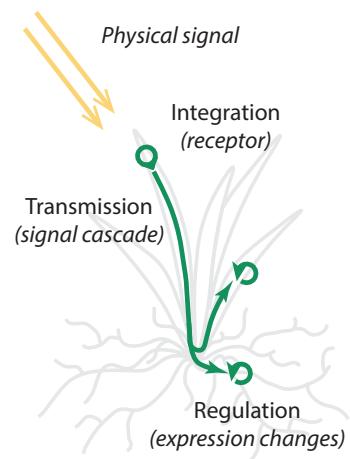


Figure 3.3: Mechanism of active plasticity. Integration of a physical (or chemical) signal, transmission and regulation of phenotype through regulation of gene expression, or post-transcription regulations.

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.

REFERENCE AND PLASTIC TRAITS

netic control (*i.e.* species-specific parameter). This means that, despite a shared rule and similar phenotypes, the plastic would be different and would depend on a species-specific parameter (right column). Phenotypic plasticity should be a form of **strategic plasticity** to be analysed differently from a growth function.

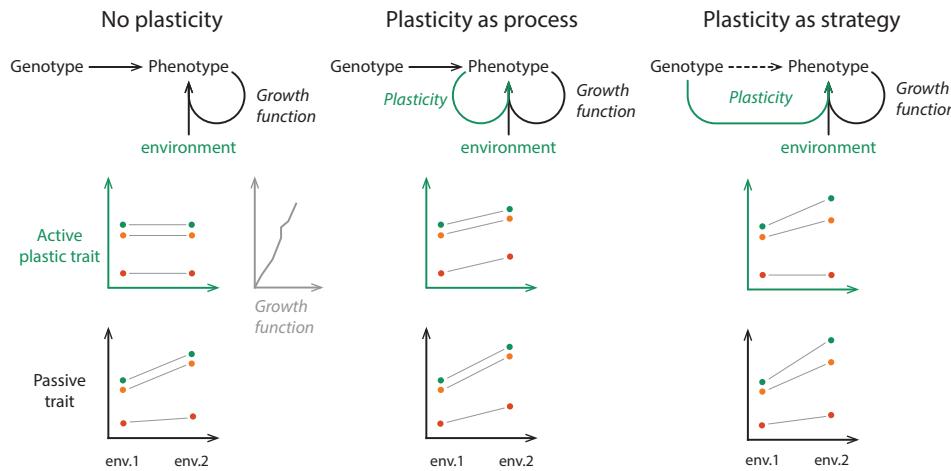


Figure 3.4: Three forms of plasticity in models. *No plasticity*, the differences in trait (passive trait such as total biomass) are explained by the growth function. *Plasticity as a process*, the active plastic traits change in the same way in both condition: the process is not just growth, but it is shared between all species. *Plasticity as strategy*, the species respond in different ways despite sharing the same starting phenotype and environments. The plasticity is a strategy determined by a genetic trait.

Only the plasticity as a strategy differentiates conceptually the plastic response with the growth response. Paradoxically, this difference is better embodied in models with reaction norms (that generally differ between species), than mechanistic models that share a same mechanisms for all plastic responses. Plasticity as a strategy is possible within models with a shared plastic response mechanism, but they require additional species specific parameters to control this plastic response. This is because these models (Lohier *et al.*, 2014) are based on the assumption that the general plant functioning can be captured by shared processes and the differences are captured between the species-specific parameters. So, it is logic in this context, if we consider the plasticity as a process different from the "growth function" only, to attribute species-specific parameters that control the plastic response. The adaptive value of this traits, and therefore of the plasticity, can now be dependent on the other traits, and the plasticity can be exposed to mutation and selection processes. While this a mid to long-term objective, it is first important to define strong plasticity mechanisms.

As mentioned, the plasticity needs a **driving rule**. In a physiological perspective, it a set of signalling cascades triggered by external stimuli. In an evolutionary perspective, it would be a sort of optimisation function. It is the work of the modeller to translate the shaping effect of the evolutionary forces, into responses that can be coded into chemical reactions and make sense in the context of the model (a plant can create an estimation of future condition, but cannot determine precisely these conditions). From this, ones can have a more practical approach, and mimic the chemical cascades, and their effects of the physiology and morphology of the plant. The **reaction norm**, that determine the new target phenotype as a mathematical function of an explicit external variable (*e.g.* the leaf thickness as response of the received light energy (Feller *et al.*, 2015)) is a good example of such approaches. But there are an infinity of functions, and the shape and the parameters of these functions, the rules, are extracted from the empirical knowledge, data or from a theory. In this case the plasticity is defined

PLASTICITY RULES: A QUESTION OF DRIVERS

by a set of rules, linking one variable with one particular traits.

But our understanding of plant physiology et ecology can also help us modelling plasticity with a more conceptual approach. The evolutionary objectives can be translated in general rules, under the assumption that the biology and chemistry of plant allow the coding of these rules. This could be seen as finalist, but make sense in an evolutionary perspective. The plant try to respect the established rules by modifying all the plastic traits. In this case, all traits follow an explicit general objective, such as the functional equilibrium (Hirose, 1987; Lohier *et al.*, 2014) or a net return optimisation (McMurtrie & Dewar, 2011). In this case, the link between the phenotype and the objective must be clearly establish in order to determine what is the best phenotype.

Defining the rules driving plasticity is a complex task. It requires to consider the plastic dimensions (traits), the available information of the external conditions (external sources of stress) and the general objective. Moreover, there is an apparent contradiction between the idea of a driving rule and the plasticity as a strategy. If the the plasticity is driven by a general rule given by strong evolutionary principles, how can species express diversity in plasticity? To have different strategies, plant can follow this general rule to a different extend, with strong plastic response and weak or null responses. This could be seen as a "trust level" in the general driving rule. Alternatively, multiple rules could compete in a same model, the species parameter determining the rule to follow would be the plastic strategy mentioned in the previous paragraph. Using a general principle to drive plasticity has the advantage to integrate all plastic responses (from root to shoot, from anatomy to physiology) in a coherent framework, and avoid incoherent responses. But these incoherent responses can a be a form of limit of the plasticity (DeWitt *et al.*, 1998; Van Kleunen & Fischer, 2005), maladaptive responses that are observed in nature. Maladaptive plasticity could still emerge from such model, because if the response are coordinated and coherent, the estimation of conditions determining the best phenotype main not be good one.

In any case, the drivers of plasticity, reaction norms or general rule, must be determined as a function of the traits of interest and the context of the scientific questions examined.

The phenotypic plasticity differ from other form of intra-specific variability by a strong and direct control of the changes in phenotype by the plant, in relation with the experienced external conditions. Such level of control can only be model by precise rules that tight the forcing variables with the response traits in a coherent framework, based on both physiological and evolutionary principles.

Modelling phenotypic plasticity as a strategy of the species requires both a framework link forcing variables and traits, and authorising differences between species. While many options are available to model this phenomenon, the choices of the modeller should be driven by the specificity of the system and the scientific question.

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, 2002; Scheiner & Holt, 2012; Scheiner & Lyman, 1989)), or better understand the cost and limits of plasticity (Auld *et al.*, 2009; Callahan *et al.*, 2008; DeWitt *et al.*, 1998), or the effect of plasticity on coexistence and community dynamics (Hart *et al.*, 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 (D. Ackerly, 2004; L. Poorter & Bongers, 2006; Wright & Westoby, 2002), conceptual (Grime, 1977; Westoby, 1998) and modelling(Kleidon & Mooney, 2000; Reineking *et al.*, 2006; Scheiter & Higgins, 2009) 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 (Feller *et al.*, 2015; Lohier *et al.*, 2014). 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 (Auld *et al.*, 2009; DeWitt *et al.*, 1998). 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(Ryser & Eek, 2000), explaining contrasting response along gradient or between experimental drought treatment (Jung, Albert, *et al.*, 2014; Kichenin *et al.*, 2013). 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. - Ryser & 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 increases 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 *et al.*, 2009; Callahan *et al.*, 2008) and ecological (Auld *et al.*, 2009; DeWitt *et al.*, 1998; Scheiner, 2002; Scheiner & Holt, 2012; Scheiner & Lyman, 1989; Van Kleunen & Fischer, 2005), limiting the extend of plasticity observed in nature and differences between species (in grasslands see Ryser & Eek (2000)).

The costs of plasticity refers to the energetic expenses the plant must pay to deploy the molecular machinery to sense the changes in conditions, transmit the signal to the response organs, and express alternative phenotypes in these targeted organs. These costs must be inferior to the benefits provided by the plasticity for any form of plasticity to emerge.

But there are also limits to the plasticity, that consist in mechanisms that prevent the plastic response to be efficient. A major limitation to the plasticity is its capacity to predict changes in conditions, and to adapt, not to the current conditions, but to the future conditions in sort of developing a better phenotype over time. This temporal dimension also highlights the risk of lag between the perception of the change and the response, that could lead to maladaptive plasticity in fast varying conditions.

Modelling a coherent plasticity requires to consider this additional physiological costs, and to consider the potential limits of the plasticity by limiting the tools to predict the future conditions to the information available to the plant.

These limitations, in addition to indicate 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

COST AND LIMITS

CONTINUOUS PLASTICITY

FROM PROCESS TO STRATEGY

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 & Frankenhuys, 2016).

This shift is also important because if genes control plasticity, plasticity can also alter evolutionary process and therefore the response to climate change(Matesanz *et al.*, 2010; Nicotra, Atkin, *et al.*, 2010; Pfennig *et al.*, 2010).

Plasticity is a complex matter, both 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.

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 sen-

SPECIES DIVERSITY

sitive 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 (Jung, Albert, *et al.*, 2014; Lepik *et al.*, 2005), 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, HilleRisLambers & Levine (2007) increase in niche difference and decrease in average fitness differences would increase stable coexistence.

The impact of plasticity mechanism on stabilizing effect is also hard to anticipate. It will likely be negative because established species may better fill any potential gap and prevent low-density positive effect and therefore invasion (Berg & 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 3.7) on species diversity that needs to be disentangled. Recent review (Turcotte & Levine, 2016) of these effects show no consensus on the effect of phenotypic plasticity on stable coexistence.

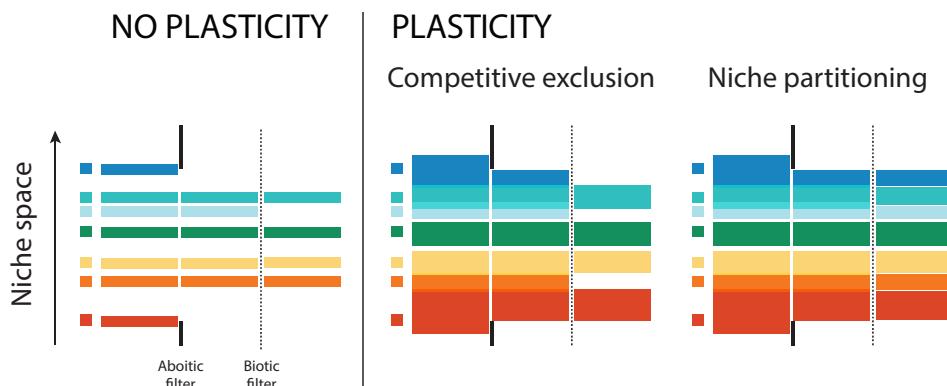


Figure 3.5: Phenotypic plasticity can affect filtering processes in diverse ways, making difficult the understanding of the role of plasticity in diversity maintenance.

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, *et al.*, 2003). A novel difficulty arises with the evidence that the identity of the competitor affects plastic response (Abakumova *et al.*, 2016; Callaway, Pennings, *et al.*, 2003), but it is likely that such interaction is related to traits and therefore impact on resource (Callaway, Pennings, *et al.*, 2003).

Species diversity often comes with functional diversity, however, phenotypic plasticity affect plant traits and is likely to affect functional diversity (Albert, Bello, *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

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are less constraint, or species experience diverse and contrasting conditions in mixtures than in monocultures.

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 Is 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.

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, Albert, *et al.*, 2014). Other empirical studies

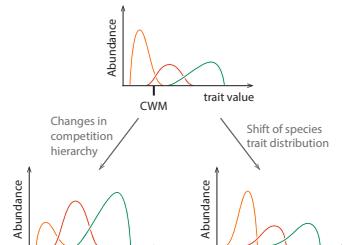


Figure 3.6: Phenotypic plasticity effects on community identity. Phenotypic plasticity can modulate community-identity response to a change in conditions by two distinct but non exclusive mechanisms: altering the competitive hierarchy and species abundances (left) or shifting the individual species identity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

show uncoupled response between above- and below-ground organs, shifting the strategy of the species (Freschet *et al.*, 2013).

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.

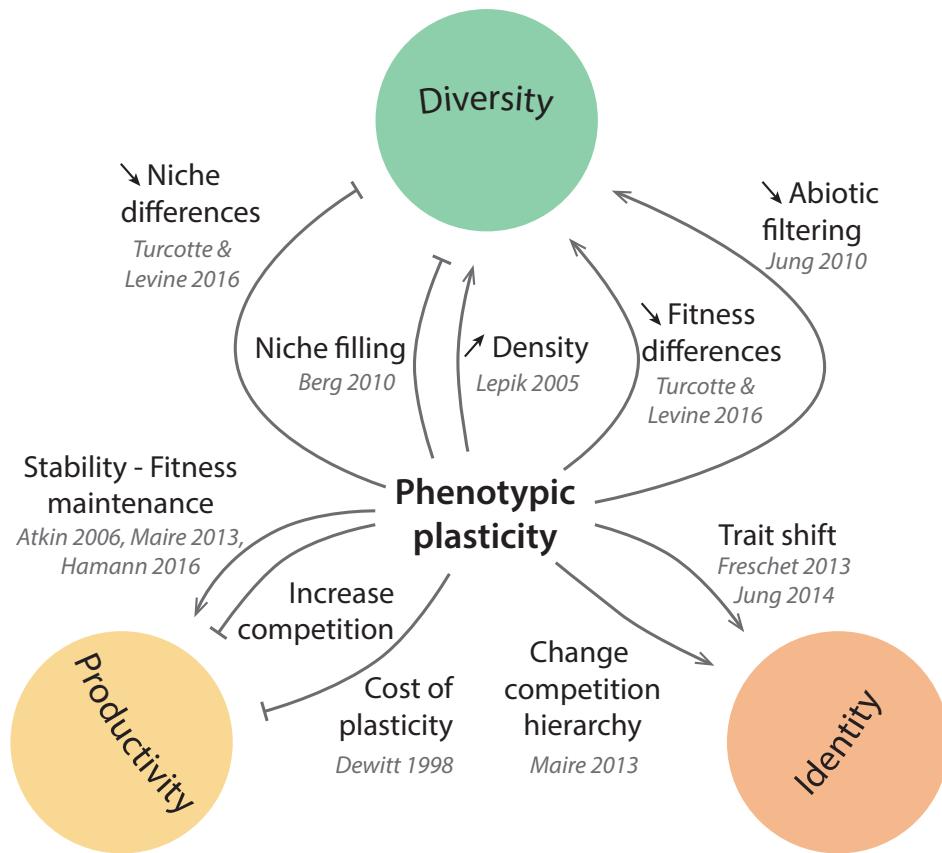


Figure 3.7: Effect of phenotypic plasticity on the three main community properties. Phenotypic plasticity can impact these properties through multiple processes that may have contrasting effects. To determine the overall effect of plasticity on community response to changes in drivers (climate and land-use)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

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. They should focus on the individual level mechanisms of competition, growth, and survival and observe the emerging patterns at the scale of the community. This can only be achieved in a constrained 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. The phenotypic plasticity being driven by the perception of the environment, it cannot be simply described by normal random distribution but should be build on a coherent framework allying physiological, morphological and evolutionary constraints. 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

The objective of this chapter is to develop the core concepts of the model, introduced in the previous chapter, and to explain the structure and design choices made during the model development. The first part focuses on the general context of alpine grasslands and some coexistence mechanisms at stake. The following part details the definition of the strategy space and the modelling of phenotypic plasticity while introducing the key concepts of species memory and individual experience. Finally, the last part is a detailed description of the model following (Grimm *et al.*, 2006) recommendations.

1 ALPINE ENVIRONMENT: CONDITIONS, RESOURCES, AND PERTURBATIONS

1.1 The scales of alpine grasslands

The **scale** is a determinant variable in the quantification of mechanisms that structure ecological communities (Bello *et al.*, 2013), and therefore in modelling approaches. It is chosen based on structures that the modeller intends to explore and determine the upper limit of mechanisms the model can reproduce. Large scales will favour geo-climatic and dispersal effects (Kleidon & Mooney, 2000) while small scales will focus on direct plant interactions processes or resource heterogeneity (Maire, Soussana, *et al.*, 2013; Soussana *et al.*, 2012; Taubert, 2014). This is true for spatial scale, but also temporal scales. Because mechanisms studies at large scales like dispersion, invasion, speciation occur over long time scales whereas mechanisms occurring at smaller spatial scale, like competition, facilitation, disturbances play a role on shorter time scales, spatial and temporal scales are often correlated. The scales are also dependent on the studied environment. There is a high contrast between highly productive environments like tropical forests and unproductive environments like mountain grasslands. The dimensions of individuals themselves are a constraint on the scales: while tropical trees grow few tens of meter high and above one meter diameter, alpine grasses do not exceed half a meter (Körner, 2003). Similar differences in the order of magnitude can be observed for life cycles between long live tree and annuals or bi-annuals grasses. The focus of this work being on plant functioning and interaction mechanisms, the scale of the model will be around the meter, while the temporal scale will be in the order of the season.

THE SCALE

The same way the scales are constraint by the size or length of the individual, the **resolution** should be close to the size of the modelled entities. The resolution is also determined by the focus of the model: interactions between individuals must be distinct and not blended to hope see the emergence of spatial patterns. Cell size and time step length should be small enough to take into account heterogeneity that is an important driver of diversity. For these reasons, the spatial resolution is set up to the centimetre and the temporal resolution to the day (can be changed but processes might not scale well).

THE RESOLUTION

Once the resolution is fixed there is always the temptation to increase the size, or scale, of the system. This should be avoided for two main reasons. (1) the increase of scale with relatively fine resolution lead to a high increase in computational power required for simulations that are already complex. (2) there is a high chance that the processes modelled at fine resolution lose their sense when scale increases. Indeed, as mentioned, the importance of processes at stake is often dependant on the scale the system is studied. The effect of higher scale processes is often taken into account in inputs or parameters. Calibration of these parameters against certain data is a way to better understand these processes (Lagarrigues *et al.*, 2015).

COMPLEXITY AND PERFORMANCE

1.2 Resources: light and water

As mentioned in the previous chapter, resource fluctuations, heterogeneity, and competition are important factors for coexistence. Unlike animals, plants mainly compete for the same resources: light, water and nutrients. Light is the source of energy that allows the transformation of inorganic carbon into organic matter through photosynthesis. Water has multiple functions in plants: transport, structural support, and oxygen supply for photosynthesis. Nutrients are used in the construction of cells and cell walls, and especially the production of proteins that act as cell machinery.

1.3 Perturbations: frost, grazing, and mowing

The most notable specificity of mountain grasslands is the climate. While there is a wide range of mountain grasslands type, the focus of this document is in French Alps. The alpine climate in France is characterised by cold winter with snow precipitations and dry summer. The growing season is relatively short and spread between May and October in low altitude, and June and September in high altitude (Körner, 2003). The particularity of this habitat is the presence of snow cover during winter that protects soil, rhizomes, and seeds from negative temperatures. Because of this, seasons are decomposed in the model based on the snow melt in spring/summer and the first snowfall in winter. While a rise in temperature is needed to allow snow to melt down, frost event can occur after the beginning of the season. Such events represent strong environmental filter for non-adaptive plants that do not invest in specific resistance mechanisms to favour early germination and growth. Therefore there is a strategic trade-off between germination date and early growth with frost resistance.

CLIMATE

Another specificity of alpine grasslands is that they are subject to changing management practices. Mountain grazing by domestic cattle was fairly common in the Alps, but changes in agricultural practices and a decrease in productivity due to drought lead to less and less grazing or mowing for fodder in alpine grasslands. These two types of management have different impacts on the community. While mowing is non-specific and favours small plants, herbivory is known to be specific when the production is greater than the grazing pressure. Leaves with high nutrient content and low structural tissues content are generally favoured because of high input and high digestibility. The grazing pressure plays as equalizing mechanisms as it favours conservative species with lower

MANAGEMENT

competitive ability.

Other forms of herbivory can happen in grassland context, but the extent of the grazing by large herbivores reduce the relative importance of this effect and allows us to ignore this diversity of herbivory sources with complex dynamics.

2 MULTI-DIMENSIONAL STRATEGY SPACE, CARBON POOLS, AND TRADE-OFFS

2.1 Multi-dimensional strategy space and allocation pools

2.1.1 The strategy space in *MountGrass*

In an ecological agent-based simulation model a species will be defined by its values for the species-specific parameters. They can be estimated from experimental data (Lohier *et al.*, 2014; Maire, 2009; Taubert, 2014) or be picked from a strategy axis (Kleidon & Mooney, 2000; Reineking *et al.*, 2006) composing a strategy space (Westoby, 1998). The diversity of the species pool will depend on the number of values for each of these specific parameters, or traits, and the number of these traits. Each trait increasing the dimension of the strategy space (Laughlin, 2014). The ambition of this model is to simulated rich plant communities, the definition of these axes is crucial. Trade-offs between traits are excellent applicants for these specific parameters as they reduce the dimensionality of phenotypes to a small number of dimensions (Díaz *et al.*, 2016; Reich, 2014; Wright *et al.*, 2004) while keeping the information of traits needed to describe the plant functioning. Trade-offs emerge from ecological and physical or biological constraints, by considering these constraints Darwinian demons are avoided.

WHAT IS A STRATEGY SPACE

While considering too many axes does not improve community description, a certain number is needed to have strategic diversity (Laughlin, 2014). This is intuitively explained by the fact that each trade-off is closely related to a particular aspect of fitness or mechanism for coexistence (*e.g.* reproduction, competitive ability, resistance to resource shortage, predation, etc.). In this model, multiple aspects of plant life are represented: germination with the germination rate for storage effect (Adler *et al.*, 2006; Chesson, 2000), dispersion with seed mass (Westoby, 1998) or tissue construction cost (Reich, Walters, *et al.*, 1992; Reich, 2014; Wright *et al.*, 2004). Main components of plant growth and life history are covered by such trade-offs and driven by mechanisms shared by all vegetation systems. Because of that, the model has a great potential of genericity and diversity. It can be easily adapted to other plant communities with specific calibration, and extended to couples of biological process and differentiation axis (*e.g.* root herbivory and associated resistance carbon pool). The the trade-offs

used in the model are detailed in the model description below¹. These axes should, in such models, be independent, (*i.e.* it is physically and biologically possible for a plant to take any position in the space drawn by two given axis) and result from physical or biological laws (ensuring that impossible strategies are indeed excluded from the model). First, it is a condition for parsimony of the model. The second and more interesting reason is that any trade-off emerging from the model should have an ecological interpretation (Maire, Gross, *et al.*, 2013).

¹ see section 4.

One way of constraining plant strategies to certain axes is to consider allocation trade-offs (Kleidon & Mooney, 2000; Reineking *et al.*, 2006). An allocation trade-off is the translation of the mass conservation rule that prevents the allocation of biomass to distinct carbon pools. If biological functions are related to organic matter pools (photosynthesis to leaves, water and nutrient uptake to roots), then the sum of biomass to invest in each carbon pool (therefore in each function) cannot exceed the total available biomass: leaving the plant with a choice on the balance between the different functions. Allocation trade-offs have the advantage to be easily implemented and be intuitive. By design, a partitioning factor value corresponds to a position on the related strategic axis. In *MountGrass*, 5 main trade-offs are captured by allocation trade-off: (1) development vs reproduction: partitioning factor between reproduction and maintenance of vegetative tissues (when plant is mature), (2) persistence vs dispersion: partitioning of reproduction biomass between persistence (storage) and production of new propagules (seed/clone production), (3) aboveground vs belowground competition: investment between shoot and root, (Kleidon & Mooney, 2000; Reineking *et al.*, 2006; Taubert, 2014)(4) slow vs fast: construction cost trade-offs between active and structural tissues in both shoot and root and (5) growth vs resistance: partitioning between stored biomass and frost resistance carbohydrates (Cai *et al.*, 2004). This last trade-off can be extended to other carbon pools of specific resistances, for example to herbivory. Modification of these coefficients during life history is a way to introduce plasticity in the model. The rules driving such changes for some of this partitioning parameters are described in the following section.

One of these trade-offs, (4) slow vs fast, is key and related to the construction cost of organs (independently leaves and roots). Highlighted at the global scale and for leaves, the Leaf Economic Spectrum (Wright *et al.*, 2004) draws a strategic differentiation axis from conservative slow species and exploitative fast species. The construction cost has long been identified as a factor of strategic differentiation in plant communities(Westoby, 1998). This strategic axis, being related to many functional traits: SLA, LDMC, LNC, leaf longevity, Amass, etc.(Wright *et al.*, 2004) is of crucial importance. First, these traits are closely related to the characterisation of plant communities and the assessment of services (Grime, 1998). Second strong links and correlations can be made between these soft traits physiological traits (Craine *et al.*, 2002; Reich, Buschena, *et al.*, 2003; Wright *et al.*, 2004). Finally, a species resource use strategy is closely related to its responses and vulnerability to changing conditions (Deléglise *et al.*, 2015; Dwyer *et al.*, 2014; Poorter *et al.*, 2009). The traits related to this trade-off play a major role both in individual growth and physiology and in community services

and response to a gradient. Therefore it is essential to the model. Analysing the underlying mechanisms for such strong trade-off is necessary to implement satisfying representation in the model.

These trade-offs between highly productive tissues with low construction cost and short lifespan called exploitative, and more conservative strategy with longer lifespan but lower productivity are mainly observed thanks to soft traits such as SLA for LNC (Wright *et al.*, 2004). Mechanistic models require traits related to physiology and organ performance (Lohier *et al.*, 2014; Soussana *et al.*, 2012), but a link can generally be done between these traits and soft traits. However, traits such as SRL or SLA are composite traits emerging from different organ properties (John *et al.*, 2017; Ryser, 1996), where tissue density and organ thickness are the main determinants. "*A necessary trade-off between allocation to structural tissues versus liquid phase processes*" has been identified by Shipley *et al.* (Shipley *et al.*, 2006) as one of the two main factors for the leaf economic spectrum to emerge. Such allocation trade-off can indeed explain differences in construction cost as the liquid phase corresponding to the "active" part of plant tissue, the cell content, have much lower dry volumetric mass than its "structural" counterpart, the cell-wall. Also, active tissues containing the protein machinery for photosynthesis and water absorption, a higher proportion of high protein concentration tissue would be correlated to higher nitrogen concentration in the organ on the "fast-slow" spectrum, along with a higher mass-based photosynthetic rate (Reich, 2014). On the other end, the structural tissues give the organ a higher lifespan (Mediavilla *et al.*, 2001; Ryser, 1996) that compensate for lower productivity (Westoby *et al.*, 2000). Such trade-off can be apply to both shoot and roots (Craine *et al.*, 2002; Reich, 2014; Tjoelker *et al.*, 2005). From that, the decomposition of organs between active and structural tissues constitutes a strong basis to model construction cost trade-offs as the main parts of the global strategy space.

A similar axis of differentiation has been demonstrated for roots (Picon-Cochard *et al.*, 2012; Reich, 2014; Tjoelker *et al.*, 2005). The necessity for independent similar axis for leaves and root can be discussed with respect to coordination between shoot and root activities. Because perfect equilibrium cannot be guaranteed in all conditions, strict coordination cannot be taken as a principle for the reduction of strategy space. Moreover, empirical results suggest small deviations from coordination are common (Freschet, Kichenin, *et al.*, 2015). The leaf economic spectrum being conserved at the intra-specific level (Hu *et al.*, 2015) is another reason to include such trade-off as it would be a good basis for phenotypic plasticity (Freschet, Bellingham, *et al.*, 2013).

The use of allocation trade-offs allows the construction of a generic multi-dimensional strategy space where a high diversity of species can potentially coexist. Because this space is based on physical laws, it ensures the non-existence of Darwinian demons and does not limit the species or individual plants to tested parameters and strategies. To be complete, the link between carbon pool allocation and physiology must be defined, respecting similar biological or physical laws.

2.2 Craft a trade-off: active and structural tissues

Allocation trade-offs offer great flexibility and are easily understood and implemented. However, when they control the value of traits (SLA or SRL) involved in multiple processes, a balance must be found to avoid that: (1) one process is ignored because it has a low relative importance for fitness (becoming useless to the model), (2) the effects of processes involved show strong response curves to the allocation and there is only one global¹ optimum. The idea behind a trade-off is that multiple positions are viable in different conditions or in association with other strategies. The leaf-economic spectrum, in addition to relying on the active-structural tissue trade-off, also requires "*an evolutionary trade-off between leaf photosynthetic rates, construction costs, and leaf longevity*"(Shipley *et al.*, 2006). This trade-off is explored in this section of the document.

In the framework of the model, plants share the same global parameters, as it should also be the case for photosynthesis parameters. Because photosynthesis relies on the exchange of gases (CO_2 , O_2 and H_2O) and the interception of light, it is related to exchange area. Considering one shared parameter for maximum area-based potential exchange rate satisfies both the need for a shared parameter and a way for plants to varying their mass based exchange rate by changing their proportion of active tissues. This is in agreement with the LES that a strong relationship between mass-based traits and limited ones for area-based variables (Wright *et al.*, 2004), and explain the first part of the trade-off between photosynthetic rate and construction cost. The second part is the relationship with the longevity. The longevity is often correlated to SLA in empirical studies, however, this is mainly explained by differences in tissue density and toughness than in thickness (another component of SLA). For this reason, we can directly link the leaf longevity to active tissue proportion. Respiration is also increased by the increase in the proportion of photosynthetic tissues (Kleidon & Mooney, 2000; Reich, 2014). We have now a trade-off between a gain function (exchange area gain by changes in densities) and a cost function (tissue turn over and respiration). This should be enough to explain different strategies (Westoby, 1998). However, the model needs internal limits to avoid the gain function to lead to only active tissue organ (or only structural). These limits are required to allow individuals or species to change position along these axes (plasticity or strategic shift). The convex shape of gain function in association with a minimal cost (minimum turn-over cost above maximum potential gain) is enough to limit the allocation to structural tissues only. To avoid allocation to only active tissue, that would correspond to an organ made of protoplasts, the cost function needs higher than the potential gain. To achieve that an exponential function is chosen. This choice ensures that the potential gain function has an optimum different from the borders.

The tissue density is only one of the dimension of the SLA, and plants also vary their thickness in response to resource gradients (Poorter *et al.*, 2009). For simplicity reason, only the density dimension will be considered in the model, while others tend to prefer only the thickness (Feller *et al.*, 2015).

To allow diversity to emerge from temporal and spatial resource heterogeneity, the potential gain (productivity) of plants must be a function of both the plant

¹ I use the term global here to designate the multidimensional space draw by the axis of interest and other variables play a role in involved process (e.g. resource availability, temperature etc...).

strategy and the external conditions. While it makes no sense to have the productivity independent from the external conditions, if it is only driven by those, then the model is either a neutral model and the plasticity makes no sense in such model, or a model where only one strategy is the best, and plasticity would just allow the convergence toward this unique optimum phenotype. There must be different strategies dominating different habitats.

This requirement is taken into account in the construction of the trade-off between the active and the structural tissues. The costs are mostly controlled by this allocation trade-off. The potential gain is not only a function of active tissue proportion but also depends on resource availability. Changes in resource level imply changes in the slope of gain function and a shift of the organ optimum for tissue allocation. This shift makes more conservative strategies more interesting when resources are scarce, while more exploitative allocation strategies are better for high resource availability. This link between optimum allocation and resource level could be used to define the best phenotype according to experience conditions, but the organ strategy cannot be disconnected from the whole plant strategy and allocation.

The phenotype (within the subspace of vegetative allocation) depends both on the individual efficiency of organs and the balance between shoot and root activity. This balance often used to model plant plastic allocation and considered between light and nitrogen (Lohier *et al.*, 2014; Soussana *et al.*, 2012). In the context of mountain grasslands and global change, the water is more important and will certainly be more variable. The integration of nitrogen as a limiting solution would allow more functional diversity but complicates the optimisation problem that is the plasticity.

2.2.1 Species memory and phenotype determination

As mentioned, the overall plant productivity is a function of three main **phenotypic axis**: the root mass fraction (RMF), the proportion of active tissues in roots (PAR), and the proportion of active tissues in the shoot (PAS). These three dimensions define a vegetative phenotypic space. The phenotypic plasticity consists of rules that drive the trajectories of the individual plants within this space to improve their performance relative to a fixed position. Modellers have to find a way to link the species-specific strategy with this starting point and the trajectories the plant can follow. This link is given by the concept of species memory of the species that translate the genetic information of the species in an information that have sense and can be manipulated.

In a non plastic context, the strategy and the phenotype are one thing, and there is no need (from the plant perspective) to associate this phenotype with the external conditions. In a plastic context, the phenotype, in addition to being linked to the overall plant strategy, is also linked to the external conditions (by the plasticity rules). There is a dependency between the plant strategy, its phenotype and the external conditions. In one direction, the conditions define an optimum phenotype (or phenotypic subspace) that best fits them. In the other direction, a phenotype corresponds to a set of favourable conditions and therefore contains these climatic conditions. This can be seen as the species **memory** of the conditions captured by mutation and selection processes. When the plant starts growing, it has no prior information on the external conditions yet but

VEGETATIVE PHENOTYPE AXIS

MEMORY OF SPECIES: A DRIVING TRAIT

expresses a species-specific phenotype by default¹. Because of the link between this phenotype and the external conditions, this starting phenotype can be expressed as a function of species strategy and expected conditions. The genetic information that defines the starting phenotype is partially expressed by the memory of the species and its strategy traits. It could be that the memory is enough to define the starting phenotype if there is an explicit function that links a set of conditions with an optimum phenotype. While this makes the concept of memory neater, it reduces a lot the possibility of diversity and supposes that evolutionary processes would have selected the best phenotype rather than the phenotypes that are able to maintain themselves. In *MountGrass*, this partial constraint, defining a subspace rather than an optimum phenotype is illustrated by the control of the root mass fraction (RMF). The balance between the shoot and root activities being key in the overall plant performance, the RMF will be determined as a function of the species memory. The other strategy traits are defined independently and characterise the strategy of the species.

Because the phenotype is defined from this memory, the plasticity can then be imagined as a modification of the information given by the memory based on the experienced conditions. The plasticity is then a balance between this prior information contained in the species genetic information - the **memory** - and further information given by the conditions lived by the plant - the **experience** - leading to a posterior image of the conditions - the **estimation** - driving the trajectory of the plant within the phenotypic space.

The concept of memory, in addition to link the starting phenotype/strategy with the plant trajectory/plasticity, also opens the door to the modelling of heritability by a meaningful alteration of this memory. If the experience of a plant does not match its species memory, it could change this value to transmit this information to new propagules.

The decomposition of organs organic matter in active and structural carbon pools makes a link between allocation and physiology and draws a subspace within the strategy space where individuals can move and change their phenotype. Limiting mechanisms restrain the viable options to realistic values along these axes. Within this space, the resource availability and external conditions play a major role in the expression of the strategy. The memory of the species offers a starting point for the phenotypic trajectories of plants driven by the plasticity rules that have to be defined.

The identification of axes of strategic differentiation enables the definition of a strategy space for the modelling of species rich communities. The main resource-use strategies within this strategy space rely on established allocation trade-offs. Because they link physiological parameters with carbon pool sizes, these trade-offs allow to model contrasted plant behaviour in a realistic way. The effect of changes on allocation strategies on physiological processes can also be modelled thanks to this explicit link.

¹ in a non plastic context, this phenotype is maintained over time.

3 MODELLING PHENOTYPIC PLASTICITY

3.1 Plasticity as a strategy: between species memory and individual experience

3.1.1 A concept of active plasticity as a strategy

The active plastic response is highly integrated (Freschet, Swart, *et al.*, 2015) and involve a lot of regulatory processes (Nicotra & Davidson, 2010). It is impossible to represent all regulatory processes involved in an adaptive plastic response (APR) (because of our lack of knowledge and their complexity). Alternatively, the concept of *integrated response* can be conceptualised. It supposes a link, or coordination, between the experienced conditions and the phenotypic response. This can be translated, in the model framework, by the existence of an explicit link between a representation of external conditions and a phenotype matching this conditions: the **allocation rule**¹. Another key work is *anticipatory*. It supposes that the plant knows, or at least have an idea of the future conditions. This is really the point of an active plastic response: change the phenotype to better match future conditions. A representation of future is also called a **projection**. The projection and the allocation rule together form the active plastic response. If allocation rule is not obvious and is discussed later(see paragraph 3.2), the idea of projection is fairly intuitive. The projection will correspond to a value for a given metric that represents the external conditions. It can be resource availability level, temperature, herbivory risk, etc... If such metrics can be given at the community scale, it makes sense to use a plant-centred measure of these variables for two reasons: (1) take into account the spatial heterogeneity, (2) plant experience of conditions is necessarily egocentric. The details on how experienced conditions are interpreted by plants in *MountGrass* are described in section 4.

Active plasticity is now represented by a projection and an allocation rule. However, how a species can control the whole process is unclear. In theory, both projection and allocation rule can be species-specific. In nature, plants generally have structurally similar regulatory processes² and responses to external stimuli are translated (and stored temporarily) thanks to the accumulation of chemical compounds. These mechanisms suggest that, while the allocation rules are mainly shared, individuals vary on the information level (i.e. the concentration of phytohormones), or in the context of the model: plant vary in projection. This control of active plasticity is supported by the model design. The number of rules that can drive the allocation is reduced and discrete, while the projection is multi-dimensional (one dimension per external variable considered), continuous and highly flexible with a reduced number of parameters³. For this reason, **projection** is chosen to be the **controlling factor** of active plasticity, while the allocation rule is fixed and shared between all species. Therefore an individual with fixed projection won't be actively plastic, despite the fact that it could express apparent plasticity because of external factors: reduced resource availability, grazing, frost damage, etc... The model has now a concept for active plastic response⁴ controlled by the projection of external condition. The next question that needs to be answered is: how do species differ in their plastic response ?

THE DECOMPOSITION OF PLASTIC RESPONSE

¹ the use of the word *allocation* is justified here since the phenotypic plasticity in *MountGrass* reduced to changes in allocation.

CONTROL OF PLASTICITY

² see box in section II 3.

³ details in paragraph *estimation of conditions* in section 4.

⁴ In the rest of the document terms *plasticity* or *phenotypic plasticity* will refer to an *active plastic response*.

3.1.2 Species specific plasticity: the balance between the species memory and the individual experience

In *MountGrass*, the projection of external conditions is the means for plants to alter their phenotype in response to changes in experienced conditions. Since the allocation (or driving) rule is shared by all plants, if the projection of external conditions is also shared by all plants, then is the response still active plasticity? The first intuitive answer is *yes* since the conceptual framework is respected and plants would react to changes in conditions that would affect the projection. But, such response would be equivalent to a direct external control of the climate on the phenotype. In such case, species would not have control over how the phenotype varies, that would be fully controlled by shared projection and shared allocation rule. This is passive plasticity. To have proper active plasticity, the species need to be able to **regulate** the plastic response. If species can regulate plastic response thanks to species-specific parameters, plasticity becomes a **strategy**. This is in agreement with Bradshaw's vision of phenotypic plasticity as a trait, or a character, subject to selection and evolutionary processes(Bradshaw, 1965; Bradshaw, 2006). How do species regulate the plastic response to make it a strategy?

SPECIES SPECIFIC PLASTICITY

Therefore, to have a proper **strategic plasticity**, the plants need to control the plastic response, so in *MountGrass* to control the projection. This modification of the projection makes the specificity of the plastic response and allows diversity in plasticity.

SPECIES MEMORY AND INDIVIDUAL EXPERIENCE

The projection is the way plants control phenotypic plasticity. A projection is an idea of the future based on available information and on the understanding of a phenomenon. Ones could discuss what is the understanding of the climate by plants, while others can focus on how to represent such understanding and state that fine molecular regulatory processes can reproduce and store such information. The focus is on the construction of the projection with respect to the different sources of information a plant has: (1) its experience of climate and external factors, and (2) its ancestors' memory¹.

While, for any given individual plant, the experience of external conditions varies in time, the memory stays fixed. There is a clear contrast between the variable experience of conditions and the fixed species memory. A way to represent different strategies and the level of control the plant apply on projection is to vary, between species, the relative weight of species memory against individual perception. This species-specific parameter, the **confidence in species memory**, sets the **stability** of the projection with respect to individual experience. The capacity to adapt the phenotype to changing conditions is directly linked to the projection changes. High confidence in species memory translates in a low amplitude of projection variations, and though in low active plasticity. The calculation of projected resource availability levels, or temperatures, are detailed in the dedicated paragraph of the model description. The key message is that the species has control on plasticity with both its confidence in species memory and the said memory that alters the projection.

¹ see paragraph 2.2.1.

3.2 Driving rules of allocation

Allocation rules are determinant in the model behaviour as it is shared by all species, and link the projection of conditions with the phenotype. The objective of the allocation is to define the target phenotype for a given individual while considering the information about the external environment and the state of the individual. It has been established that the current model will rely on a projection of the conditions to establish such target phenotype. Therefore, the allocation rule characterises the mathematical link between this projection, the current state of the individual and the target phenotypes. The definition of the target phenotype resides in the solving of the system defined by the allocation rule, the projection and the individual state. Depending on the allocation rule, the system can be strongly constrained by the allocation rule, reducing the number of solution, but also leading to strong convergence between individuals sharing the same projection, and difficulties to model diverse communities. Alternatively, a less constrained link between the projection and potential target phenotype would define a sub-space solution rather than an unique solution. An addition rule is then required to define the target phenotype. This additional rule can be function of the individual state (*i.e.* phenotypic distance) reducing the convergence between individuals and allowing more diverse communities. While the allocation rules can have strong effects on the plastic behaviour of modelled plants, the main objective of these rules should be to improve fitness. Comparison to empirical pattern should allow us to test the validity of such rules.

One of the assumptions of the plasticity developed in this document is the existence of a tight relationship between experienced condition and fitness. A subsidiary assumption in the implementation of this plasticity is that this function can be captured, or modelled, by the same functions that drive plant growth. In other words, simulating individual growth, using the estimated/projected conditions as parameters, day by day, is enough to capture the link between environmental conditions (experienced by the focal plant) and plant growth¹.

A determining allocation rule would try to explicit this link function and optimise it. In other words, find the phenotype that maximises the gain function. While evolutionary processes allow the integration over time of the effects of phenotypic changes, it is not possible to consider this dimension without a long-term projection of the conditions. So the temporal dimension is excluded, and the maximisation of the daily gain is hypothesised to maximise the gain over time. On the other hand, a directive function would identify a subset of acceptable phenotypes. Then, an additional selection function is required to select the target phenotype within this subset. A sensible criterion of selection is to consider the distance between the current and the alternative phenotypes to select the target one. The elements around the choice of the gain functions, determining the optimum phenotype or subset, and the eventual selection function are discussed in the following description of the model.

The driving rule of plasticity defines whether or not the choice of the phenotype is fully determined by the projection of external conditions or also constrained by some species-specific parameters. The effect of this balance between projection and parameters has a large influence on the model behaviour. In any case, the projection is the main control on individual plastic response to change in conditions, offering possibilities to modulate individ-

¹ that takes here the value of fitness proxy

ual plasticity despite an allocation rule shared by all species. The role of both projection and allocation rule will of particular interest during the analysis of the impact of phenotypic plasticity of plant growth and community dynamics.

While the representation of plasticity as a strategy increases both model potential species diversity and potential diversity of response (Kichenin *et al.*, 2013; Ryser & Eek, 2000), plasticity itself may reduce diversity. Indeed, plasticity lead to changes in phenotype in response to condition changes, while these phenotypic changes are unlikely to be identical for all individuals, their general convergence points will probably be similar. Plasticity is a mechanism that is likely to contract the space of expressed values for plastic traits. Therefore, it is hard to analyse the effect of plasticity on functional diversity without disentangling the direct effect on the expressed trait values, and the indirect effect of changes in performance and interactions. Nonetheless, some external mechanisms¹ can prevent convergence of phenotype: (1) changes in competitive hierarchy may lead to differences in individual experience of conditions, (2) specificity of the external driver, e.g. selective herbivory of more digestable species, (3) diversity of position of the target phenotype.

Asides from these external mechanisms, there are internal controls of active plastic response: the projection and the plastic allocation mechanisms. It is easy to imagine numerous projections and allocation mechanisms, however, they are susceptible of emerging only if they have a positive impact on fitness overall. Considering the diversity of plastic response is a research question in itself, and I will not try to answer it in this document. Nevertheless, the progress in the understanding of the effect of plasticity on performance and potential diversity this work provide will certainly help further work in that direction. In this context, the use of species-specific control over the projection of conditions is already a step forward and prevent total convergence². Indeed, without considering multiple allocation algorithms within the same community, having the plasticity as a strategy (Bradshaw, 2006) (controlled by a species-specific trait, as opposed to many existing individual-based-models) allows interesting questions to be addressed. The question of the cost of plasticity is central in the understanding of this mechanisms (Auld *et al.*, 2009; DeWitt *et al.*, 1998), and could lead to mechanisms of co-selection between resource use or reproductive strategies with plasticity strategies. The first step in this direction consists in looking at how plasticity can have different impacts on the performance of species with different strategies (conservative versus exploitative).

THE PARADOX OF PLASTICITY

¹ impacting the drivers of plastic response, not the response itself

² in addition to directive allocation mechanisms, see below subsection 3.2

3.2.1 On the difficulty to match strategy and conditions.

As mentioned in the previous section, the framework of plasticity developed in this document relies on a strong link between condition estimation and the phenotype, that is supported by the assumption that similar link exists between condition experienced by the focal plant and its fitness. If this assumption is correct, then the initial phenotype (or default phenotype) should match the optimum phenotype defined by this link expressed by the allocation rules and the species-specific memory of conditions. Otherwise, an artificial phenotypic drift could be observed: the phenotype could change to meet the optimum defined by the allocation rule, without any change in the projection of the conditions. This could allow modelling ontogenetic shift but complicates the computation

WHY MATCH PHENOTYPE TO MEMORY

of plasticity costs and the analysis of the effects of the plasticity. One main difficult emerges here: because the processes involved in plant growth are numerous and complex, it is not possible to determine analytically what phenotype is the best (considering the memory of conditions). This point is discussed in the following paragraph as the understanding of the component of plant performance is a first step to understand the model's behaviour and plasticity mechanisms. Ones could compute the convergence phenotype for a given memory of external conditions for each possible memory combinations, and map the phenotype to the memory. This solution is a good alternative to an analytical solution when the later is not possible, but it comes with the disadvantage of a very high computational cost that is prohibitive for calibration procedures. When an allocation rule is the only directive, defining a starting phenotype is easier because an ensemble of phenotype satisfies the coherence between the memory and driving rule.

Limiting the plasticity costs and adding additional steps to reduce the phenotypic drift should allow the exploration of the different allocation rules and the effect of the phenotypic plasticity.

The projection of external conditions, driving the plastic allocation of organic matter, lies on a balance between species memory and individual experience. Its design makes of plasticity an axis of strategic differentiation alongside the other strategy axes. Thanks to this innovative design, the model can be used to examine the ecological relevance of plasticity in different conditions and in association with different strategies. The effect of allocation rules and projection stability can be explored independently or conjointly for a better understanding of the relative importance of allocation and plasticity.

4 ODD DESCRIPTION OF THE MODEL *MountGrass*

This document is a detailed description of the *MountGrass* model. This description is based on the ODD protocol of Grimm et al. The model is inspired by multiple other forest and grassland models (for grassland models see particularly Taubert (2014) and Lohier (2016)). It differentiates itself from these models by the incorporation of phenotypic plasticity in a generalizing framework for plant functioning. This allows it to be used to both to explore the fundamental effects of phenotypic plasticity the dynamics of rich grass communities and the impact of the phenotypic plasticity on plant interactions. The general approach and the practical details are further detailed in this document.

4.1 Model overview

4.1.1 Model purpose

The development of *MountGrass* is motivated by the need for a flexible tool to explore the complex dynamics of mountain grassland communities, in the context of global change. This tool should, by a better understanding of community

dynamics and representation of plant strategies and interaction, also help in the assessment of ecosystem services in new conditions. We believe that to capture the dynamic of such communities, we need to understand and represent first the individual response of plants to fluctuating levels of resources, and the impact of plants on the resources. Individual responses and relative impact should follow general rules of plant physiology but also integrates specific behaviour based on the species resource use strategy and individual characteristics. Therefore the model should allow following distinct individuals from different groups (e.g. species) in a spatially explicit environment where they compete for resources.

Moreover, since we focus on the community levels, coexistence mechanisms are important and we should include a certain number of these if we want to maintain diversity to observed levels. These mechanisms include: multiple resources competition (water and light), spatial and temporal heterogeneity of resource levels, strategic trade-off between species, perturbation mechanisms (frost, management), link to meta-population, etc...

The model is built to try to satisfy conditions to reproduce and explore mountain grassland community dynamics. In the current version of the model, a generalist approach has been privileged, and focus on some coexistence maintenance mechanisms and integration of phenotypic plasticity framework. In this state, the model has to be seen as a toy model with good generalisation potential. The link between to ecosystem services are not included, but we can easily imagine to compute them from the community trait distribution. All processes and mechanism are detailed below.

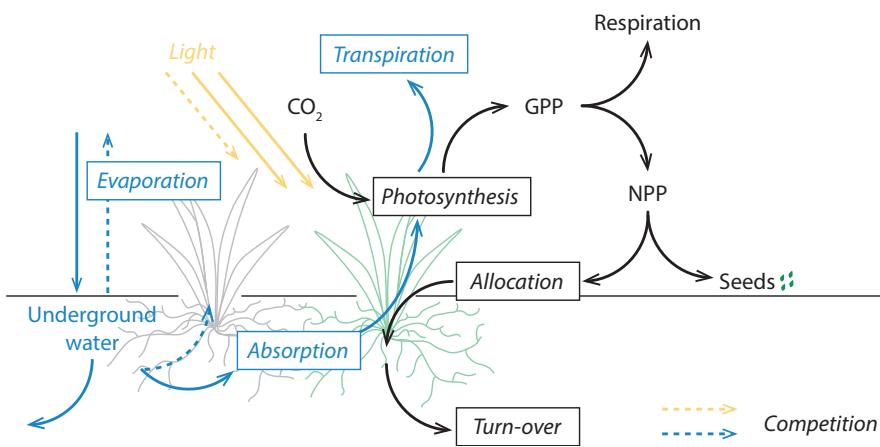


Figure 4.1: Model overview. **Water** and **carbon** cycles are represented. Processes are represented framed and in *italic* by contrast with pools that are not framed and in regular fontface. Dashed arrows indicate loss of resource (for the **focal plant**) due to competition.

4.1.2 State variables

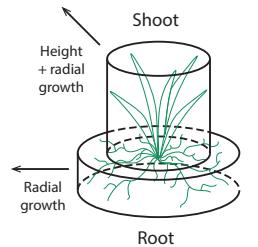
In mountain grasslands individuals (tillers) generally do not grow big and interact only with close neighbours and form little patches. And thus it is possible to represent a rich community at a fairly small scale (\approx dm or m), but the spatial resolution should be relatively fine (\approx cm) to capture inter-individual interactions. Because the model is intended to explore climate change impact on mountain grasslands, it can run on multiple growth seasons separated by snow-covered periods, but must also integrate the intra-seasonal variations at a daily scale. Mountain weather (mostly temperature) is known for its large hourly variations, it would, however, require too much computational power

SCALES

to consider such variations. Modelling such hourly variations also implies the modelling of fine scale water regulation processes. To avoid the high cost of hourly variations, the assumption that plants regulates their water exchanges to maintain fairly constant water use efficiency (WUE) is made. Therefore, the physiological processes are modelled on daily time-step.

The plants are described in the model by state variables described in table 4.1. The best way to understand how plant are represented is to imagine two homogeneous cylinders on top of each other, the shoot cylinder varying in radius and height representing the light acquisition (and shading) zone, and the root cylinder varying only in diameter (because of shallow soil in mountain ecosystems) representing the water acquisition zone. These cylinders are centred on cells of the torus simulation plan to simulate periodic boundary conditions and avoid edge effects.

PLANTS



In addition to classic variables (age, position, height, diameter, shoot and root biomasses) the plants are described by traits, that can be species-specific or non-specific, others are variable (SLA, SRL) and depend on particular traits that are unique to this model: the **ratio between active tissue and structural tissue** (in shoot and root) (variables $\frac{act}{str\ ag}$ and $\frac{act}{str\ bg}$ in table 4.1). This couple of traits come from the evidence that numerous trade-off observed in leaves can be explained (at least partially) by this allocation trade-off between active tissue producing organic matter, but increasing respiration, and structural tissue that increase tissue lifespan.

Figure 4.2: Plant geometry and growth axis.

Table 4.1: State variables of individual plants

Variable	Description	Unit
x	x position on the grid	cells
y	y position on the grid	cells
age	age	days
sp	species	-
BM_{ag}	above-ground biomass	g
BM_{agsen}	senescent above-ground biomass	g
SLA_{sen}	senescent above-ground biomass	$cm^2.g^{-1}$
BM_{bg}	below-ground biomass	g
stem	stem biomass	g
$\frac{act}{str\ ag}$	above-ground active on structural biomass ratio	g/g
$\frac{act}{str\ bg}$	below-ground active on structural biomass ratio	g/g
h	height	cm
r	shoot radius	cm
r_r	root radius	cm
$light_{exp}$	above-ground potential resource availability	$gH_2O.\text{leaf area}$
$water_{exp}$	below-ground potential resource availability	$gH_2O.\text{root area}$

Plants are characterised by state variables that describe them individually, but they also share common characteristics with individuals of the same group, (we will refer as *species* to talk about this group in the rest of the document even though it could be a group at another scale (i.e. population, clones). These

SPECIES

species are the groups present in the meta-population and that can invade the simulated ecosystem. There are described by multiple traits characterising the strategy of the species (table 4.2).

Table 4.2: Species traits

Trait	Range (close range)	unit	trade-off or strategy
seed mass	(0.00001 - 0.001)	g	seed output vs seedling productivity
maturity	-	green biomass	flowering time vs reproduction potential
fract_dev	0-1 (0.05-0.6)	-	blooming vs persistence
fract_rep	0-1 (0-1)	-	reproduction vs persistence
geometric constant (k_g)	(0.1 - 20)	-	competition sensitivity vs self-shading
plasticity stability	0-1 (0.8-1)	-	genetic information vs experience
initial water resource	(0.001 - 0.05)	$gH_2O.cm^{-2}$	water resource niche
initial light resource	(0.001 - 0.05)	$gH_2O.cm^{-2}$	light (in H_2 equivalent) resource niche
$\frac{act}{str} ag,d$	(0.03 - 0.3)	$g.g^{-1}$	active vs structural tissue
$\frac{act}{str} gg,d$	(0.03 - 0.3)	$g.g^{-1}$	active vs structural tissue
mean temp.	(0 - 5)	°C	early vs late germination
germination rate	0-1 (0.5 - 1)	-	good season bet-hedging
thickness	(0.012 - 0.05)	cm	WUE vs light efficiency (not in this version)

The seed-bank is the transition state between the different seasons. Individuals may persist thanks to stored resources, but they can also reproduce by the production of new individuals. A lot of grasses use clonal reproduction, in addition, or replacement of sexual reproduction. This type of reproduction is characterised by a persistent link between the newly produced individuals and the parent one that allows the two to communicate and exchange resources. Such dynamics are complex and costly to represent as the link between ramets must be stored and strategies defined for the resource distribution (Soussana *et al.*, 2012)) for more details on clonal growth modelling). To avoid too much complexity, it is possible to approximate the representation of clones to big seeds with little dispersion around the parent plant¹. For this reason, reproduction mechanism is reduced to sexual reproduction mechanism with the production of "seeds". Seeds are stored in the seed-bank and only defined by their species and positions.

SEED-BANK

¹ This would take advantage of dispersion kernels. Not implemented in the current version. Dispersion is uniformly random within the simulation plan

The soil is an important aspect of the model as it drives (with the precipitations) the water competition between individuals. It is however limited, as in numerous vegetation models, to a grid characterised by its capacity to retain water, and its depth. Only the first component (water retention capacity) is spatially variable and is described by the critical water content (minimum soil water content), the saturation water content (maximum water content, the water non absorbed leaves the system we assume the same root depth for all species), and the current water content (temporally variable, depending on competition, precipitation and evaporation, between the critical and the saturation water content) only dynamic variable among the three.

SOIL

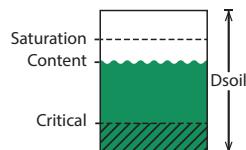


Figure 4.3: Soil section.

4.1.3 Process overview and scheduling

As mentioned the model runs at a daily step to capture individual responses to conditions and over multiple seasons to capture long temporal dynamics. Some processes occur (or are evaluated) at the daily time-step, some at the season time-step. The following ordered list presents the different processes and the scheduling over days and season of one simulation.

One season can be divided into the following parts:

- *germination*: marks the beginning of the season when the ground is no more snow-covered;
- *growing season*: consists in daily processes like competition, production of organic matter (OM), allocation, and death lottery;
- *reproduction-invasion-persistence*: marks the end of the season when the first persistent snow-fall occurs. OM invested in reproductive tissues turns into seeds that are sampled to create the seed-bank. Seeds from the meta-population may integrate the seed-bank. Persistent perennials loose most of their biomass but storage (and eventually stem) and regrow from stored organic mass at the beginning of the following season.

The *growing season* part consists in all processes evaluated every day of the growing season. These processes are:

- *light competition*: the individual potential photosynthetic activity is computed based on average daily light and shoot properties;
- *water competition*: evaporation and the individual water update (and potential water uptake) are computed based on potential transpiration, water availability and potential evaporation;
- *production*: respiration and production are computed to give the net productivity in OM;
- *senescence*: based on lifespan a part of tissue is no longer active.
- *death*: death of individuals based on their age and their desiccation stage (number of consecutive days with negative growth).
- *allocation*: allocation of produced OM to the different carbon pools of the plant.
- *grazing/cutting*: (optional) grazing or cutting of plants to a certain height. The grazing can be selective.¹

4.2 Design concepts

4.2.1 Design concepts

This part clarifies the rules that drive the dynamics of the model.

The purpose of the model is to understand the rules that drive the community responses. We tried making the community dynamics emerge from the underlying processes of plant growth, resource use, and reproduction. That means that population dynamics are at least partially emergent from the surviving and reproducing individuals. *Partially* emergent because it depends on the invasion



Figure 4.4: Seasons cycle in MountGrass.

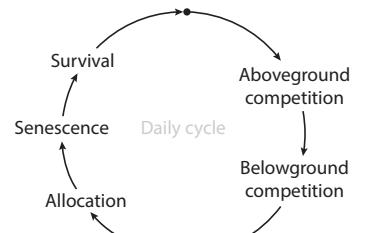


Figure 4.5: Processes in order during the daily cycle.

¹ remarks in grey are features or components implemented in the model but not used and-or calibrated.

EMERGENCE

rules applied to the system. The traits and biomass distribution that describe the community are completely emergent from the individual traits exposed by the individuals and their relative biomass and abundance.

Plants have in theory many options to adjust their phenotype and increase their fitness in response to changes in environmental conditions (resource availability, temperature, ...). High diversity of mountain grasslands suggests that multiple strategies coexist and that individuals do not change to converge toward a unique strategy. These strategies are set up at the species level by the species-specific traits (see table 4.2). Therefore, individuals may only adapt morphological traits but not strategic traits (unless there is an epigenetic mechanism added). These morphological traits are the relative biomass of shoot and root, the relative proportion of active and structural tissues in each leaf, and roots (controlling respectively the SLA and SRL and the overall resource acquisition cost)¹. Geometry traits (distribution of leaves and roots within space) are not considered plastic as grasses have far less control over their geometry than forbs or trees. Root distribution plasticity has been shown to greatly improve the individual and community productivity (Gemini article), but to keep the model (and implementation) simple we will ignore root distribution plasticity and foraging strategies to focus on allocation problems instead of spatial distribution questions. Shallow soils and relative small rooting zone are also arguments to ignore spatial distribution plasticity for roots.

In the model, the realised fitness can be estimated as the capacity of plants to maintain themselves or their descendants through time. It emerges from the productivity, allocation to storage or reproductive carbon pools, and survival. Assessing fitness as the average number of persistent individuals is, however, a bit hazardous in simulations limited in time and to a relatively small spatial scale. Plus, plants cannot easily make a prediction of such variable to adjust their phenotype. They need a proxy function for fitness that integrates measures of external conditions to evaluate the best strategy to develop. As said above, this strategy should be a composite between the species strategy and individual adjustment specific to the individual experience of the environment. Plant fitness is estimated by individual plant thanks to a gain function integrating current phenotype, species strategy, and projection of future conditions. This gain function can take multiple forms and be more or less constraint. In the context of the model, the function should include a measure of productivity that relies on the principle of functional equilibrium - that is the allocation of organic matter to maintain the balance between the shoot activity (transpiration) and root activity (water uptake). This equilibrium can be achieved by changes in shoot:root ratio only, or also changes in active over structural tissues ratio. Further details about the gain function are discussed in the dedicated paragraphs (4.3.3). A more complex form of functional equilibrium incorporating nutrients (like nitrogen) could be added to the framework of this model.

Adaptation or plasticity mechanisms imply that agents have an insight of what will be the future. In *MountGrass* we consider that plants have two main sources of information. The first source of information is the genetic information. Indeed, the evolutionary process of genotype selection has led to the selection of genotypes adapted to the local conditions. This selection relationship can be seen as a link between environmental conditions and genetic information.

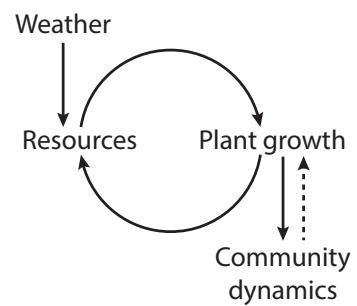


Figure 4.6: Population dynamics emerging from plant growth and weather.

ADAPTATION

¹ and optionally the proportion of stored OM dedicated to frost resistance and not to growth

FITNESS

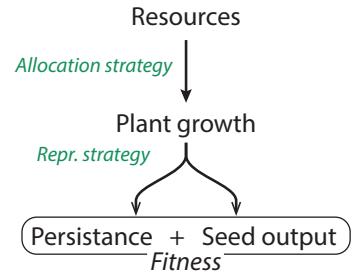


Figure 4.7: Fitness emerges from the plant growth and the plant reproductive strategy.

The plant growth is the result of the interaction of the resource levels, the plant strategy, and the competitors.

PREDICTION

Because plants cannot fully predict future environmental conditions, they grow following (at least partially) the plan contained in genetic information that match conditions where previous generations grew in. This is an internal *a priori* information about the external conditions. If the conditions where the seed grows change from the conditions its genotype has been selected for, the genetic information does not fit the environmental conditions is not sufficient enough to build a working phenotype. In this case, if the plant has a plasticity capacity, it can integrate the second source of information, in the form of the experienced conditions, to its "a priori" and forge a new estimation of what conditions will be. One question emerges to this idea is: how to create an image of future conditions and how to balance the genetic *a priori* information with the experienced information? This balance can be described by a term of "reactivity" that describes the relative weight of genetic and experienced information. A reactive species will give a higher weight to experienced condition information, whereas a stable species will give a higher weight to genetic information.

The way the two source of information are brought together and used to define the plant phenotype is at the core of plant strategy and is the main feature of the model *MountGrass*.

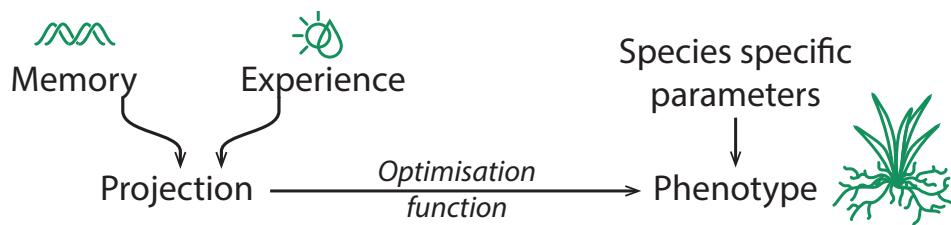


Figure 4.8: Genetic and perceived information are both considered to determine the phenotype.

4.3 Details

Further details on daily mechanisms are described in the following paragraphs.

4.3.1 Initialisation

The model doesn't need particular initialisation if the state of the community species pool, the seedbank, and the soil are given as inputs. Otherwise, a set of $E(n/s)$ individuals are created from a set of s species (randomly generated if not given) and randomly positioned on the soil grid, where s and n are respectively the number of species and the approximate number of individuals within the grid. Soil grid is also randomly generated within default ranges for critical and saturation water contents then slightly smooth, and homogeneously filled ($filling = \frac{w_{cont}-w_{crit}}{w_{sat}-w_{crit}}$).

4.3.2 Inputs

MountGrass needs system state information (individuals, species, seed-bank and soil) and climate data. If the state of the system is not completely given, then the complete state is generated in the initialisation. The daily climate data at must contain the following fields:

- *date*;
- *radiance*, in $\text{Watt} \cdot \text{m}^2$;
- *precipitation*, in mm;
- *mean temperature*, in K;
- *mean day temperature*, in K;
- *min temperature*, in K;
- *max temperature*, in K;
- *relative humidity* in %;

Vapour pressure deficit is then computed from temperature and relative humidity.

The climate data must explicitly differentiate the seasons (delimited by the first day of the year without snow and by the first day of the second semester with snow).

4.3.3 Submodels

Individuals from the seed-bank randomly germinate according to their species-specific germination rate. Germination consist of investing a percentage (*mob* parameter) of the seed mass into shoot and root biomass according to default traits. This is coupled with a round of random seed death following uniform law of parameter *seed_{surv}*. Living non germinating seeds stay in the seed-bank until the next season.

GERMINATION

Daily processes

Light competition is central to all vegetation models as it constrains the photosynthetic activity and so plant growth. To avoid costly calculations of ray propagation we assume vertical homogeneous top radiation. Relief and orientation effects are taken into account in the computation of irradiation data.

LIGHT COMPETITION

Light competition sub-model allows the calculation of individual potential photosynthesis activity and light at soil surface for evaporation calculation.

Competition for light is calculated independently for each pixel, potential photosynthetic activity is then aggregated at the individual level. Each pixel can be seen as a column of homogeneous layers containing at least one individual (top layer). For each layer, the light transmission is computed based on leaf density.

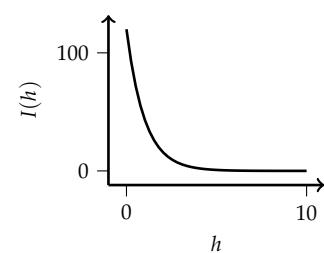


Figure 4.9: Light interception as function of leaf layer height.

$$I(h) = I_0 e^{-LAI(h)} \quad (4.1)$$

where $LAI(h)$ is the cumulative LAI at the bottom of layer l (between h and $h + \Delta_h$) defined as the homogeneous layer delimited by the top of consecutive individuals in the same pixel. The LAI is calculated like this:

$$LAI(h) = LAI(h + \Delta_h) + \Delta_h \cdot \text{pix_width}^2 \sum_{i \text{ in } l} d_i \cdot \text{coverage}_{i,p} \quad (4.2)$$

where d_i is the individual leaf area density corrected by the coverage ($0 < \text{coverage} < 1$) of the pixel p by the plant i , $\Delta_h = (h_l - h_{l-1})$ is the height of the layer l .

Following Thornley and Johnson, the potential photosynthetic leaf activity is calculated as:

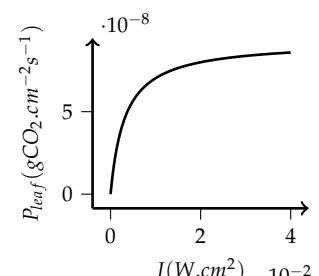


Figure 4.10: Photosynthetic saturation function.

$$P_{leaf}(h) = \frac{\alpha \cdot I_{leaf}(h) \cdot P_{max}}{\alpha I_{leaf}(h) + P_{max}} \quad (4.3)$$

where $I_{leaf}(h)$ is the light absorbed by the leaf at height h , α the initial slope of the light response curve and Pm_i the maximum photosynthetic rate per unit of area and unit of time. I_{leaf} is the radiance at the leaf surface, derived by correcting the radiance at the top of the layer following the equation used in Taubert with the extinction and transmission coefficients k and m :

$$I_{leaf}(h) = \frac{k}{1-m} I(h) \quad (4.4)$$

The equation (4.3) can be integrated over the leaf surface by mixing it with equations (4.1) and (4.2) to give the total potential photosynthesis for layer l in pixel p :

$$P_{leaf}(p, l) = d_i.coverage_{i,p} \cdot \Delta_h(l) \int_{h_{bottom}}^{h_{top}} P_{leaf}(h) \quad (4.5)$$

the total leaf potential photosynthesis is then calculated as follow:

$$PS_{pot} = \sum_{p \text{ in shoot}} \sum_{l \text{ in pixel}} P_{leaf}(p, l) \quad (4.6)$$

Potential photosynthesis must then be converted to potential transpiration to define the water demand. The conversion from photosynthesis to transpiration is done by dividing the potential photosynthesis by the water use efficiency (WUE). The potential activity of leaves are also dependent on the regulation of stomata so the transpiration can be written:

$$transp = \frac{PS_{pot} \cdot g_{red}}{WUE} \quad (4.7)$$

Photosynthesis depends on gazes exchanges at the leaf surface. These fluxes result from relative concentration in carbon dioxide and water, and from the stomatal conductance. Stomatal conductance is reduced and limits productivity when vapour pressure deficit is too high ¹. A linear relationship describe this relationship:

$$g_{red} = 1 + VPD_{g_red} \quad (4.8)$$

STOMATAL REGULATION

¹ g_{red} is set to 1 for current version to avoid potential problems between allocation and regulation

Potential evaporation is calculated for each pixel depending on the light at soil surface:

$$\beta = 0.25 * (1 - \cos(\frac{\theta}{\theta_{sat}} * \pi))^2 \quad \text{if } water_{cont} \leq water_{sat} \quad (4.9)$$

$$\beta = 1 \quad \text{otherwise} \quad (4.10)$$

$$PET = 0.0023 \cdot \sqrt{(T_{max} - T_{min})} * (T_{mean} + 17.8) \quad (4.11)$$

$$evap = PET \cdot \beta \cdot I_{surface} \cdot daylength \quad (4.12)$$

EVAPORATION

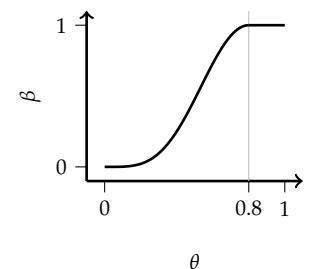


Figure 4.11: Evaporation limitation function.

Water competition is also computed at the pixel level. To determine the water uptake, first the individual water demand is computed as the minimum between the transpiration and the potential water uptake. Transpiration demand per pixel is easily calculated by dividing the total potential transpiration by the volume in the pixel $V_{i,p}$ over the overall root volume V_i . Water potential uptake is the product of root area in the pixel and root water uptake rate reduced by the water availability reduction factor U_{lim} , leading to the water demand for individual i in pixel p :

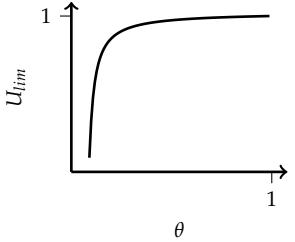
$$transp_i(p) = transp \cdot \frac{V_{i,p}}{V_i} \quad (4.13)$$

$$Wpot_i(p) = Root_{area}(p) \cdot U_{max} \cdot U_{lim} \quad (4.14)$$

$$Wdem_i(p) = \min(transp_i(p), Wpot_i(p)) \quad (4.15)$$

$$(4.16)$$

WATER COMPETITION



where, the limitation function U_{lim} is defined as in (Reineking *et al.*, 2006):

$$U_{lim} = \exp \left(\beta_\theta \left(\frac{1}{\theta_s - \theta_{crit}} - \frac{1}{\theta - \theta_{crit}} \right) \right) \quad \text{if } \theta < \theta_{crit} \quad (4.17)$$

$$= 0 \quad \text{otherwise} \quad (4.18)$$

Figure 4.12: Water uptake limitation response function to soil saturation

The total water demand per pixel is then the sum of all individual water demand of the pixel and potential evaporation. If the total water demand exceeds the total water availability (W_{av} product of water content and soil volume in the pixel) then the available water is distributed proportionally to the individual demand.

$$Wup_i = Wdem_i \cdot \frac{Wdem_{total}}{\min(Wdem_{total}, W_{av})} \quad (4.19)$$

The potential water uptake ($Wpup$), non limited by the transpiration is calculated the same way but considering $Wdem_i = Wpot_i$ in equation (4.19).

Because the water competition is computed at the pixel level, there is no compensation between two pixels containing respectively not enough and too much water.

No radial flow of water between pixel is implemented in the model. This simplification leads inevitably to edge effects, but allows simpler implementation and is partially covered by the effect of the pixel size. Indeed, increasing pixel size would have similar effect in the pixels at the border of the rooting zone than radial flow because it would increase the potential water pool plant has access to.

Once potential and realised transpiration and water uptake are computed, plant productivity can be calculated.

Following previous vegetation models, the respiration is decomposed in growth respiration and maintenance respiration. The first is function of trait values, biomass and temperature:

$$R_m = \left(R_{act} \cdot (Act_{ag} + Act_{bg}) \right) \cdot daylength \cdot T_{effect} \quad (4.20)$$

where R_{act} is the respiration rate of active tissues, and Act_{ag} and Act_{bg} are the active biomass pools in shoot and root.

PRODUCTION, AND RESPIRATION

Net Primary production (in CO_2 equivalent) can then be calculated the difference of GPP and respiration, then converted in OM production thanks to tissue carbon content (under the assumption of fixed carbon content for leaf and roots between species):

$$NPP_{carbon} = (1 - R_g). (WUE.min(w_{up}, trans_p) - R_m) - BM_{total} * Pl_{cost} \quad (4.21)$$

$$NPP_{OM} = NPP_{carbon} \cdot (12/44) / TCC \quad (4.22)$$

Here R_g is a fixed parameter but is set to 0 if the difference between gross productivity ($GPP = WUE.min(w_{up}, trans_p) - R_m$) and maintenance respiration is negative. Pl_{cost} is the plasticity cost as calculated in the dedicated paragraph below.

Temperature has a effect of plant activity, this effect can be modelled by a bell shape function around an optimum value of 20 °C. See Lohier for details.

TEMPERATURE EFFECT

The projection of environmental conditions is central in any implementaion of phenotype plasticity. Differences between the current perception of environment and the projections lead to adjustment of phenotype to increase fitness. In the model *MountGrass*this projection results from hte averaging of two key concept: memory and perception. The latter is relatively simple to understand and corresponds to the perceived resource availability computed as the mean potential exchange rate per unit of area (total leaf or root area) and per hour(the hourly measure is used instead of daily measure to simulate the ability of plant to perceive the photoperiod. This is an easy way of taking into account one aspect of seasonality without complicating the model. However, it also reduce the range of memory and its impact to determine the phenotype, as an additional information would be needed to define the optimum phenotype: the day length).:

CONDITION ESTIMATION

$$light_{exp} = \frac{transp}{exchangearea_{ag}} \quad (4.23)$$

$$water_{exp} = \frac{W_{up}}{exchangearea_{bg}} \quad (4.24)$$

$$(4.25)$$

The former is related to the species (or group) history and result from processes of selection and acclimation. It is the default projection of resource availability when the plant is not plastic.

$$light_{est}(t + 1) = (1 - \tau).light_{exp}(t) + \tau.light_{memory}.daylength(t + 1) \quad (4.26)$$

$$water_{est}(t + 1) = (1 - \tau).water_{exp}(t) + \tau.water_{memory}.daylength(t + 1) \quad (4.27)$$

Because these are supposed to be expected conditions for the future, other formulation can be used instead of an average that is likely to introduce a lag in estimations. For example the following equation allow for a more stable projection that better fits the slower process of plant physiology adjustments:

$$light_{est}(t + 1) = ((1 - \tau_{react}).light_{exp}(t) + \tau_{react}.light_{est}(t))((1 - \tau_{amp}) + \quad (4.28)$$

$$\tau_{amp}.light_{memory}).daylength(t + 1) \quad (4.29)$$

with τ_{amp} and τ_{react} being respectively amplitude and reactivity where only τ_{amp} is used in the first equation. Such solution could limit sensitivity and phenotypic

instability. IN addition, such formulation would also better capture the accumulation of stress signals and would lead to a softer and more stable phenotypic shift.

The estimation of external conditions as expressed here is then used to select the best allocation scheme during the allocation process. Limited here to levels of two resources (light and water), this estimation equation could be extended to other mechanisms such as herbivory risk, frost risk, humidity impact on water pressure deficit.

Allocation is primordial in plant development and ontogeny. The following paragraph detail the implementation of the plastic allocation in *MountGrass*.

ALLOCATION

Maturity: For most of plants the development cycle is divided in two phases of different durations: the vegetative phase when plant growths organs to gather resources and product OM, and the reproductive phase when plant take advantage of these organs to accumulate carbon and invest them in reproduction mechanisms. Plants are considered mature (they switch from vegetative to reproductive phase) in *MountGrass* when the phenologic variable has reach a species specific threshold. The phenologic variable can be either the age, the height, the biomass, degree.days, in the current version total living biomass is used as trigger for reproductive phase.

Allocation to supporting tissues: Even-though grasses do not grow tall vegetative parts like trees, some grow vertically and they are exposed to stronger winds than most of forest. Therefore they need structural supports¹. Not all grasses grow stem, but they'll have stronger central vein in their leaves to structurally support the weight of leaves. In addition shoots and roots also need supporting tissues for water transport, for this reason the minimal mechanical support needed is calculated as a function of total living biomass:

$$support = \alpha \cdot (BM_{ag} + BM_{bg})^\gamma \quad (4.30)$$

where α and γ are allometry coefficients.

At each time step we must determine what fraction of new OM will be allocated to tissues growth while the remaining will support these need tissues. This leads to an optimisation problem numerically solved by the function `uniroot`.

¹ This supporting tissue mechanic is also needed to avoid exponential growth rate.

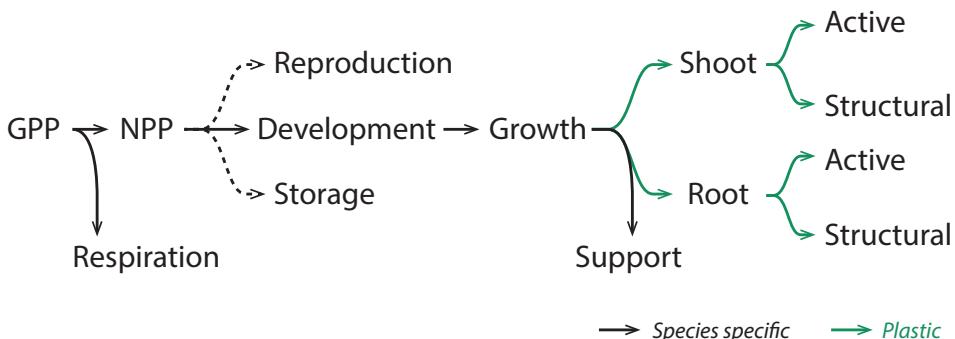


Figure 4.13: Allocation of produced organic matter to different processes and pools.

Allocation to organs: Allocation of produced organic matter is central in vegetation as it shapes the plant and define the strength of the different organs. There are multiple ways to model the distribution of produced organic matter between the plant organs. We believe that such mechanism has great impact on individual development and response to external conditions, and so on community dynamics. To explore the role of this mechanism, multiple options are implemented. The different allocation algorithms are summarised in table 4.3.

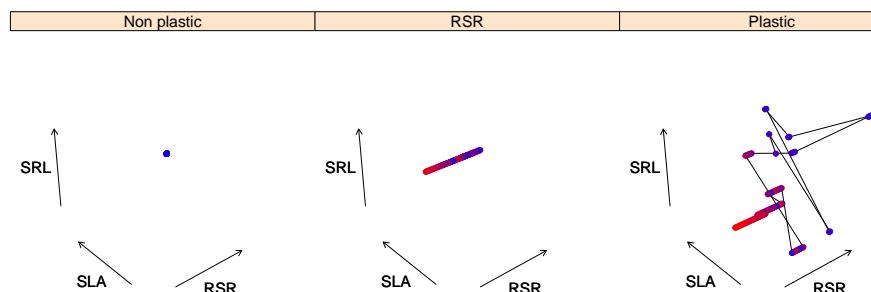
There are two major components in the allocation algorithm:

- the objective function;
- the plastic dimensions.

The *objective function*: it is the function that give an fitness estimation or gain metrics for any given phenotype. This function is used to compute the optimum phenotype (phenotype at which the function is evaluated at the maximum value), or rank alternative phenotypes¹.

The *plastic dimensions*: they are the dimensions along which the individual can move. The space defined by these dimensions is the phenotypic space within which each individual plant can look for an alternative phenotype. They do not necessarily fully define a phenotype since some dimensions of the individual's phenotype can be fixed².

The objective of this step of the model is to solve the objective function with



of the 3D space. The *plastic* panel shows the shifts in plant phenotype within the whole 3D. The high variations are caused by early high growth rates supported by the consumption of stored organic matter (seed).

the unknown variables being the plastic dimensions (RSR, SLA and SRL). In case of simple equations an analytical solution could be used to find an optimum³. However, because the analytical solutions are already non trivial and the model is likely to evolve, a numeric solving method is adopted. Random phenotypes are sampled within the possible range of phenotypes considering the actual position of the plant within the phenotypic space, and the available organic matter to allocate. First the organic matter is partitioned between shoot and roots, then it is divided between active and structural tissues for both organs.

Other options have been explored, but the non continuity of the system caused numerical solver unstable. Because the allocation is random and extreme allocation patterns are considered, high growth rates in combination with a low number of samples can cause unstable allocation patterns, especially when the

¹ in this case, if not all possible phenotypes are tested, the solution might be only a local optimum. This is the case in *MountGrass*.

² either by shared parameters of species specific ones.

Figure 4.14: Trajectories of a plant in the trait space depending on the plastic dimensions explored. The RSR panel illustrates plasticity on only one axis (RSR or RMF)

³ under the condition that such optimum exists. The design of the model should ensure that.

plants benefit from high growth rates due to stored organic matter. Higher number of samples and lower growth rates decrease this phenomenon.

Algorithm	Objective	variable RSR	variable SLA-SRL	stochastic
No plasticity	—	○	○	○
Equilibrium	functional eq.	●	●	●
Eq-Fixed	functional eq.	●	○	●
Optimisation	instantaneous gain	●	●	●
Optim-Fixed	instantaneous gain	●	○	●

Table 4.3: Allocation algorithms implemented in *MountGrass*

No plasticity allocation: this allocation is very similar to classic vegetation model where the biomass is allocated to the different carbon pools according to species specific parameters. But *MountGrass* differs from other models by the order of the different steps of growth. In this model, the senescence comes between the allocation step and the resource competition-production steps ¹. The partitioning coefficient are directly computed from species default trait to maintain the phenotype after senescence.

Fixed trait allocation: The fixed allocation supposes the allocation on OM to maintain trait values to fixed species specific values. The shoot:root ratio may however change to maintain functional equilibrium. The shoot root ratio is derived from the following equation of the functional equilibrium:

$$SLA \cdot BM_{ag} \cdot light_{est} = SRL \cdot BM_{bg} \cdot water_{est} \quad (4.31)$$

$$\frac{BM_{ab}}{BM_{pg}} = \frac{SRL}{SLA} \cdot \frac{water_{est}}{light_{est}} \quad (4.32)$$

where $light_{est}$ and $water_{est}$ are the estimated resource availabilities.

Plastic trait allocation: Another approach to allocation is to try to optimize phenotype based on a fitness proxy. This proxy can be the sum of NPP, tissue turn-over loss and plasticity cost. But in a complex model like *MountGrass*, plant performance is function of multiple aspects:

- individual organ efficiency;
- relative mass of each organ;
- balance between organ water exchange activities.

And this could be extended to herbivory or frost risks. To take into account all these components, and take advantage of having all processes already made explicit by the implementation in the model, the daily processes of senescence and production are recalculated according to the **estimation of conditions** and the plant phenotype. This function is used to rank different alternative phenotypes (algorithm detailed below).

Plastic trait equilibrium: An alternative approach can be easily derived from the previous one and extend the principle of the first: the functional equilibrium with plastic traits. This approach consists in using the same algorithm as before but rank phenotypes with a function negatively correlated to the difference between estimated shoot and root activity. Such mechanism would nonetheless require the algorithm to look for close solutions within the allocation space to avoid convergence or drift from species strategy. Having non zero cost of plasticity in this approach should limit the drifting of the plant phenotype.

¹ see plastic allocation algorithm for explanation

Fixed trait optimisation: This algorithm takes the idea of the optimisation algorithm but limits the plastic traits to the RSR ratio. If we can expect similar response than the fixed trait equilibrium if we suppose that the equilibrium is the main aspect of plant performance, global efficiency being considered in this case the result may vary.

Alternative phenotypes are computed from the actual phenotype and random uniform distribution of available organic matter to the main active and structural carbon pools of the plant.¹ ... This algorithm has the advantage of being relatively cheap compared to other optimization functions, however, its performances are variables and it is very sensitive to the number of samples used. As a consequence there is a trade-off between model stability and performance as a function of the number of samples (*i.e.* alternative phenotypes) considered.

PLASTIC ALGORITHM

¹ talk about the order senescence production, and the way exchange rates are computed.

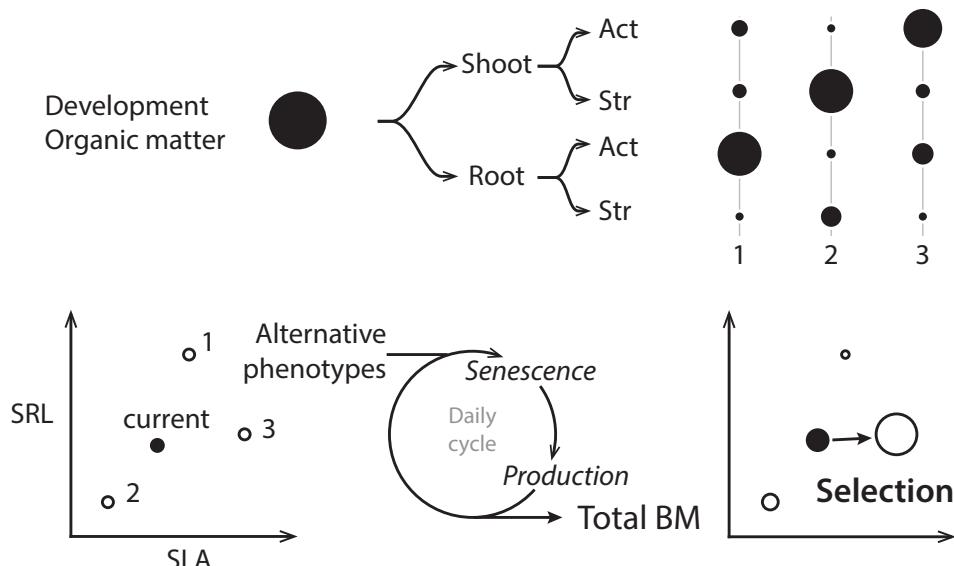


Figure 4.15: Algorithm for the evaluation and selection of randomly generated alternative phenotypes.

The limits and costs of plasticity have long been discussed in the related literature. If *MountGrassis* intended to be used to examine ecological costs and limits, it has to include physiological aspects of plasticity limits. There are two physiological processes involved in the mechanism of altering a phenotype based on changes in external conditions: sensing and signalling. 'Sensing' relates to the capacity of the individual to perceive environmental conditions. This is related to the capacity of the individual to perceive the environment and should, therefore, be considered constant over time. To take into account the cost of precise sensing, the first component of the plasticity cost is proportional to τ .

The other component is related to the capacity of the plant to transmit this knowledge of conditions to change the development plan toward a new phenotype. This cost is proportional to the carbon-based distance (calculated as the difference between proportion of active tissues) between the default phenotype and the alternative (during allocation algorithm) or current phenotype.²

Plasticity cost is the sum of both component and is proportional to the total biomass since most of the tissues should have the appropriated cell machinery

PLASTICITY COST

² We could imagine cost based not on the default, but the previous phenotype, but it would have lead to large phenotypic shifting and convergence.

and are affected by plasticity.

$$pc_{maintenance} = (1 - \tau) * pc_m \quad (4.33)$$

$$pc_{plasticity} = d_{traits} * pc_p \quad (4.34)$$

where d_{traits} is the Euclidean distance between default phenotype and the alternative phenotype in the space defined by the proportion of active tissue for shoot and for roots.

Plasticity in trait suggests that trait values are modified in time. Because plants are described by single values (e.g. one SLA value for all leaves), this values must be updated after the plastic allocation. This values could be updated as the average of old tissue value weighted by old biomass and new tissue value weighted by the freshly produced biomass. This, however, would work only if active on structural tissues ratio linearly linked to others traits. This is not the case, it is then simpler to consider that organs have uniform active and structural distribution. This hypothesis suggests that whenever the allocation scheme change, old tissue reallocate their own biomass to follow the new scheme. Nevertheless, to avoid full plasticity allowed by this hypothesis, the changes in trait carbon pool sizes are limited by the produced biomass available for plant development.

following the following survival probabilities:

From this, supposing homogeneous distribution of active and structural tissues within an organ allows to directly link the size of the carbon pools to average traits by the following relationships:

$$SLA = \frac{1}{(th.p_{act_{shoot}}.\rho_{as} + th.(1 - p_{act_{shoot}}).\rho_{ss}).V_t} \quad (4.35)$$

$$SRL = \frac{1}{(s_r.p_{act_{shoot}}.\rho_{ar} + s_r.(1 - p_{act_{shoot}}).\rho_{sr})} \quad (4.36)$$

Senescence is the process of ageing of tissues. This process usually occurs at the scale of an individual organ (e.g. a leaf), however, *MountGrass* does not consider organs independently because it would be complex and computationally expensive to follow multiple leaves and roots for all individuals. So the process is considered homogeneous over all tissues. To emulate the senescence process senescence is calculated from the tissues lifespan, giving :

$$sen_{leaf} = \frac{1}{LLS} \quad (4.37)$$

$$sen_{root} = \frac{1}{RLS} \quad (4.38)$$

Because *MountGrass* does not contain any mechanism preventing plant from growing only active tissues¹, it is necessary for this cost function to make this strategy unreliable. The is then expressed as follow:

$$LLS = LSs_{s0} * (1 - p_{act_{shoot}}^{LLS_1}) \quad (4.39)$$

$$RLS = LSr_{s0} * (1 - p_{act_{root}}^{RLS_1}) \quad (4.40)$$

where LLS and RLS are respectively the leaf and the root lifespans calculated as negative log-linear relationships with the proportion of active tissue.

TRAIT UPDATE

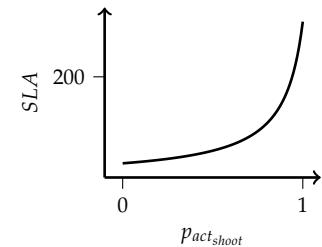


Figure 4.16: Specific Leaf Area as a function of the proportion in active tissues in shoot

SENECENCE

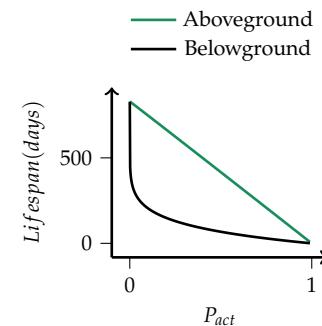


Figure 4.17: Lifespan of organs as a function of proportion of active tissues.

¹ it was intended to make the WUE negatively correlated to the amount of structural tissue per area.

Root senescent tissues disappear from the system. Information about senescent aboveground biomass is stored, but senescent biomass effect of light competition is ignored in this version because as it is implemented senescent tissues appear early in plant development and have large negative effect on light absorption.

To the natural senescence and artificial cost of having only active tissue, an additional component can be added to the turn-over rate: the negative NPP. In case of negative NPP, the biomass will be taken from the already allocated following the shoot:root ratio. This can lead to a lower overall productivity (negative growth during unproductive periods) but also changes in the equilibrium if tissue have different efficiencies.

Death is modelled as in Reineking (Reineking *et al.*, 2006). Age and desiccation (negative NPP) are the two reasons why a plant can die. The two death mechanism are simulated by independent random lotteries following the following survival probabilities:

$$P_d = \exp \left(- \left[\left(\frac{des}{\alpha_d} \right)^{\gamma_d} - \left(\frac{\max(des - 1, 0)}{\alpha_d} \right)^{\gamma_d} \right] \right) \quad \text{if } NPP \leq 0 \quad (4.41)$$

$$= 1 \quad \text{otherwise} \quad (4.42)$$

$$P_a = \exp \left(- \left[\left(\frac{age + 1}{\alpha_a} \right)^{\gamma_a} - \left(\frac{age}{\alpha_a} \right)^{\gamma_a} \right] \right) \quad (4.43)$$

State of dead individuals is store until the end of the season when seeds are stored in the seed bank. Seeds of dead individuals then join other seeds.

Sexual & clonal reproduction: reproduction is handled at the end of the season. To limit the number of parameters reproduction is limited to the division of the invested biomass in reproduction by the species-specific seed biomass into a round number of seeds (the number of seed per plant could also be a differentiation axis). Clonal reproduction is not explicitly represented but can be mimic with bigger seeds and by adding a dispersion process around the parents. The seeds then are added to a potential seed-bank. This potential seed-bank is sampled, after eventual invasion, and merged with the existing seed-bank.

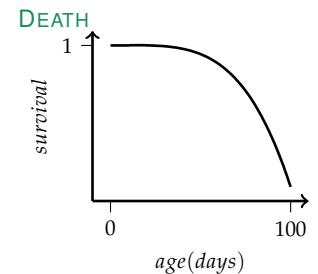


Figure 4.18: Age related survival probability function

REPRODUCTION & PERSISTENCE

Persistence Some grasses are perennial and persist over the cold season. This is allowed in the model by investment in storage tissues instead of reproductive tissues. At the end of the season, marked by the first snowfall, these plants (with non-null storage biomass) lose their living and supporting biomass, but will regrow from a large pool of store organic matter.

Explore management effect on the community is one of the aims of *MountGrass*. The management of mountain grassland will be explored only of the aspect of biomass removal, as productivity changes can be explored by changing the parameter values as the nutrients are not explicitly modelled. The management sub-model is not detailed here but it is based on the mapping of biomass and target trait (e.g. the fraction of structural biomass as a proxy for digestibility). Both cutting and grazing can be modelled but require management plan in the form of calendar of management operation and a cutting height or harvest ob-

GRAZING/CUTTING

jective.

4.4 Limitations and problems

4.4.1 Link to real world and data

The generalized framework introduced in *MountGrass* allows to create a rich community in a high number of dimension strategy space, it, however, comes with downsides.

One of the first problems is that some parameters (not explicitly detailed here) are hard to access (e.g. tissue density of active, or structural, tissue). It makes the calibration long as the incertitude for some parameters is very high. This is problematic when calibration is made difficult by a large execution time (see subsection below).

Another issue with such model is that the high dimensionality of the species strategy space allows a lot of different strategies that are not viable. This could be overcome by selection mechanism over multiple plots, but again require a lot of simulation. Moreover, there are dependencies between viable strategies and parameter values that make it hard to restrict meta-community to viable species to set-up calibration runs.

It is possible to extract summary statistics from the model output and compare them to information from collected data making calibration and community analysis easy. However going from the data to feed the model is harder, indeed without a great knowledge of a species it is hard to define its representation within the model framework. To do so would require the knowledge of the plasticity capacity to set the reactivity, anatomical traits to define default ratios of active over structural tissues, and climatic niche to define the *a priori* estimation of external conditions. Without making a direct association with real species, it is possible and interesting to try to reproduce some strategies and explore their response to various conditions.

4.4.2 Technical problems

The model is implemented in R with some limiting function using RCPP to speed up the process. Simulations are fairly slow compare to theoretical C++ equivalent code. The main problem is the choice of the data structure. Indeed agents are stored in data.frames that are often modified with the `mutate` function, that makes the implementation much easier and the code readable, but slow down the execution due to constant condition checking on operations. This makes calibration routine methods almost impossible to use as they demand a very number of runs to be efficient.

The slowness of the model also limit to simple algorithms for the research of favourable positions in the allocation space.

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IV

INDIVIDUAL PERFORMANCE: STRATEGY AND PLASTICITY

The chapter contains the main results of simulation experiments at the individual scale. It provides insights on the impact of the plastic allocation algorithms on individual growth patterns and potential effects on community properties.

The first part is dedicated to the parameter filtering and the study on individual growth in a stable environment. The second part examines responses of individual root strategies to two gradients of water availability: (1) with constant influx but differences in mean influx to simulate spatial heterogeneity, (2) with a shared mean influx, but contrasting rates of reduction of precipitation to simulate the reduction of the available resource during the growing season.

1 MODEL PROPERTIES AND INDIVIDUAL RESPONSES

The first part of the chapter is dedicated to the parameter filtering process, the sensitivity analysis and basic model behaviour.

1.1 Parametrisation and sensitivity analysis

Calibration, or **parametrisation**, is an essential step in the development of an agent-based model. ABMs are often characterised by multiple processes, and thus parameters, at individual levels. The results of these processes (depending on parameter values) from numerous individuals combine to produce the group or community behaviour. Because there are interactions between the processes and between the agents, the overall behaviour of the group (often the subject of interest) is sensitive to these parameters. For the same reasons, an incredible variety of results could be produced with ABMs if the parameters were not chosen in order to produce sensible responses to simulated conditions. The aim of the calibration is to determine the best values for the model parameters, from the *a priori* knowledge of the processes and parameters, and the comparison with data. This step often goes along with a sensitivity analysis that determines the relative sensitivity of variables of interest to specific parameters.

Because of their nature, ABMs often model processes for which the parameters are either unknown or hard to access, because they are at the individual scale. In such cases, advance calibration techniques like pattern oriented modelling (Grimm *et al.*, 2005; Hartig *et al.*, 2011) can be developed. However, such method requires a high number of simulations and relatively precise simulation parameters. Because the implementation in R makes the model relatively slow, and because available datasets, despite being very interesting lack information on sensitive parameters, a less robust but less expensive approach is chosen: **parameter filtering** at the individual scale. The focus of the part of this work on the individual growth and the will for more individual-centric approach also support this choice.

For similar reasons of computational cost, the **sensitivity analysis** is realised *a posteriori* on calibration runs.

1.1.1 Method

Pot data consists in total biomass and root:shoot ration (RSR) data of 11 species grown in pots by Peterson and Billings (Peterson & Billings, 1982). This dataset has the advantages of being grass species grown in a described steady environment with two conditions of watering with measures of essential components of growth: biomass and RSR.

POT DATA

Simulated plants grow in square pots 9 cm wide and 12 cm deep. The soil is characterised by the following parameters: critical soil water content: $0.1m^3.m^{-3}$, and saturation water content: $0.1m^3.m^{-3}$. The simulation time of 111 days of 15 hours is divided between the growing phase of 48 days and the treatment phase when plants are watered (soil saturation), either once a week or once a day. The light level and water influx are simulated following the experimental conditions (Peterson & Billings, 1982) by a lighting of 1850 Watts per square meter, and soil saturation. Plants have default geometry parameters, reproduction is ignored and it is assumed that plants do not stop their growth.

POT SIMULATION

The whole filtering process has been implemented in R. Model parameters are sampled following the LHS method (from `lhs` package) within parameter ranges (described in table 1.2) defined both thanks to the literature and constraints dictated by desired behaviours from the model. When necessary the sample is log transformed. Because of the strong relationship between exchange rate parameters and cost of exchange area, exchanges rates parameters are expressed on a mass basis for sampling then transformed into an area basis for the model. To avoid extreme RSR ratios, the ratio between the mass-based exchange rate parameters is limited between 0.1 and 10.

PARAMETER FILTERING PROCESS

As explained in the previous chapter, species-specific parameters are required to model plant growth. These parameters are sampled at the same time that the parameters of the model, according to ranges detailed in table chapter III, 4.2. Once the parameters are generated, a first filtering is applied to save simulation time and avoid unrealistic trait values. The computed initial trait values considered out of range (see table 1.2 for ranges extracted from LES data (Wright *et al.*, 2004) in the alpine biome) are excluded, modifying the initial distribution of the parameter values (see figure 1.2). These two steps lead to the creation of a list of n independent parameter sets that are then used for individual pot simulations following Peterson & Billings (1982) experiment setup.

The results from the finished simulations (i.e. the plant lives until the end and do not exceed model's internal size limits) are then compared to the experiment data species by species. The parameters of logistic distributions are computed from the species means and standards deviations for RSR and total biomass. The use of this distribution form is justified by the intrinsic form of the RSR variable and the need to reject negative values for total biomass variable. A parameter set is accepted for one species if it lies within a 95% range of the calculated distribution for both RSR and total biomass in wet and dry conditions.

The parameter filtering procedure is applied on the three main allocation algorithms: *non plastic*, *fixed-equilibrium* and *plastic-optimisation*.

The relative importance of variables in the selection process is investigated with the packages `randomForest`. A random forest analysis (depth = 5, number of trees = 300) is performed on a balanced dataset composed of all selected pa-

SENSITIVITY ANALYSIS

Table 1.1: Global parameters of *MountGrass* with units and extreme values used during the parameter filtering process.

name	min	max	unit	full name
u_max	0.36	10	cm ³ .cm ⁻² .h ⁻¹	Maximum root uptake rate
beta_o	0.002	0.2	AU	Soil absorption limitation strength
P_max	0.00001	0.0001	gCO ₂ .cm ⁻² .s ⁻¹	Maximum photosynthesis
alpha	0.00001	1.0001	AU	Photosynthesis curvature
mob	0.0005	1	fraction total green biomass	Maximum growth rate
m	0.1	0.5	AU	Leaf light transmittance
r_g	0.1	0.5	gC.gMO ⁻¹ .h ⁻¹	Growth respiration rate
r_i	0.003	0.03	gC.gMO ⁻¹ .h ⁻¹	Active tissue respiration rate
ls_so	5.7658	7.9628	day	Log of maximum shoot lifespan
ls_s1	-1.2325	0	day	Shoot lifespan slope
ls_ro	4	7	day	Log of maximum root lifespan
ls_r1	-1.5	0	day	Root lifespan slope
sd_s_rate	0.05	1	per year	Seed survival rate
WUE	0.001	0.01	GCO ₂ .gH ₂ O ⁻¹	Water Use Efficiency
LCC	0.39	0.5	gC.gOM ⁻¹	Leaf carbon content
alpha_d	10	30	AU	Drought mortality
gamma_d	1	3	AU	Drought mortality
th	0.0124	0.0437	cm	Leaf thickness
s_r	0.0019	0.05	cm ²	Root section (area)
rho_as	0.005	0.1	g.cm ⁻³	Volumic mass of shoot active tissue
rho_ss	0.8	1.5	g.cm ⁻³	Volumic mass of shoot structural tissue
rho_ar	0.005	0.1	g.cm ⁻³	Volumic mass of root active tissue
rho_sr	0.8	1.5	g.cm ⁻³	Volumic mass of root structural tissue
vt_s	0.7	0.75	AU	Volume occupied by the tissue in total leaf volume
k_os	0.001	0.01	cm ³ .cm ⁻³	Shoot volume occupancy
k_or	0.01	0.5	cm ³ .cm ⁻³	Root volume occupancy
k	0.4	0.6	AU	Light extinction parameter

trait	min	max	unit
SLA	20	400	cm ² .g ⁻¹
SRL	1000	15000	cm.g ⁻¹
LLS	10	400	days
RLS	100	1200	days

Table 1.2: Extreme values of traits related to exchange area per biomass and organ longevity for both shoot and root.

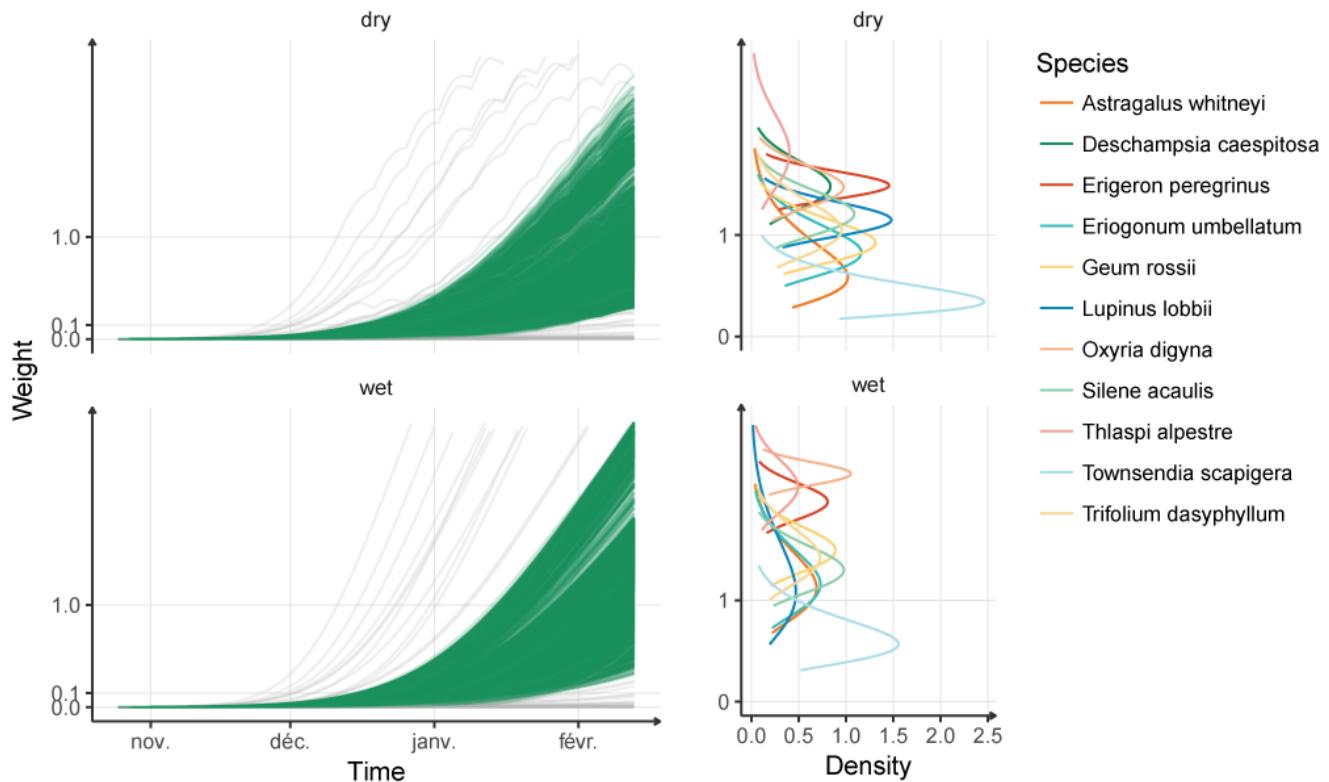


Figure 1.1: Comparison of simulated weights with distribution of weights of real alpine species for contrasting conditions.

parameter sets and a random sample of rejected sets of equal size. Importance is assessed on the results of the random forest.

1.1.2 Results

Parameter filtering process resulted in the selection of a low number of parameter sets (below 0.2%) for each allocation algorithm (table 1.1.2). This number is below the sum of accepted parameter sets per species because a parameter set can match to multiple species. Not all species contribute to the same extent to the filtering process. *Astragalus whitneyi* accounts for a high percentage of accepted parameter sets, while no parameter set could match 2 species (*Oxyria dignya* and *Deschampsia caespitosa*). The former is characterised by wide distribution in both conditions for the two variables of interest (weight and RSR), while the latter shows relatively tight distribution with little overlap between the conditions for both variables (see figure 1.1 for comparison between simulations and data for total weight).

SELECTION RATE

Despite the low selection rate, a difference can be noted between the *fixed-equilibrium* algorithm and the two other algorithms with an accepted rate of 0.14 % against 0.09% and 0.10% (table 1.1.2). This difference cannot be explained by a significantly better selection rate for specific species, but rather by higher rates for all species.

Most of the parameter sets are not shared between the algorithms (*i.e.* around respectively a third and a quarter of accepted parameter sets are shared between *non plastic* allocation and *fixed-equilibrium* allocation calibrations), despite that, the distribution of parameter values that are not shared are very similar and do

Table 1.3: Acceptance rate per species for the 3 main allocation algorithms. Because some parameter sets match multiple species, the total number and rate of accepted parameter sets is lower than the sum of accepted parameter sets per species. All rates are given in %.

species	non plastic		fixed-eq		plastic	
	n (2M)	rate	n (2M)	rate	n (200,000)	rate
Silene acaulis	227	0.02	396	0.04	55	0.03
Trifolium dasypphyllum	271	0.03	317	0.03	45	0.02
Geum rossii	51	0.01	72	0.01	12	0.01
Thlaspi alpestre	342	0.03	360	0.04	59	0.03
Deschampsia caespitosa	-	-	-	-	-	-
Eriogonum umbellatum	500	0.05	805	0.08	118	0.06
Townsendia scapigera	593	0.06	930	0.09	107	0.05
Astragalus whitneyi	1570	0.016	2424	0.24	318	0.16
Lupinus lobbii	678	0.07	868	0.09	123	0.06
Erigeron peregrinus	1	<0.01	-	-	-	-
Oxyria digyna	-	-	-	-	-	-
Total	4233	0.43	6172	0.62	837	0.42
Accepted	924	0.09	1416	0.14	200	0.10

not show any clear pattern (data not shown).

Out of the 31 parameters, 6 show graphical response of selection rate (see figure 1.2), and only u_{max} and P_{max} present a possible optimum different from limit values. The relative importance of the parameters is better explored in sensitivity analysis.

A total of 12 parameters show a relative influence on selection rate for at least one of the algorithm. These parameters are divided between model parameters and species parameters. Species parameters show influence only for the *non plastic* allocation algorithm. Model parameters express relatively similar importance for all three algorithms. The respiration rate of active tissues (r_1) is the most sensitive parameters (see figures 1.2 and 1.1.2). Other sensitive parameters are related to water availability (β_0), organ exchange rates (P_{max} and u_{max}) and soil coverage by roots (ρ_{ar} and k_{or}).

SENSITIVITY ANALYSIS

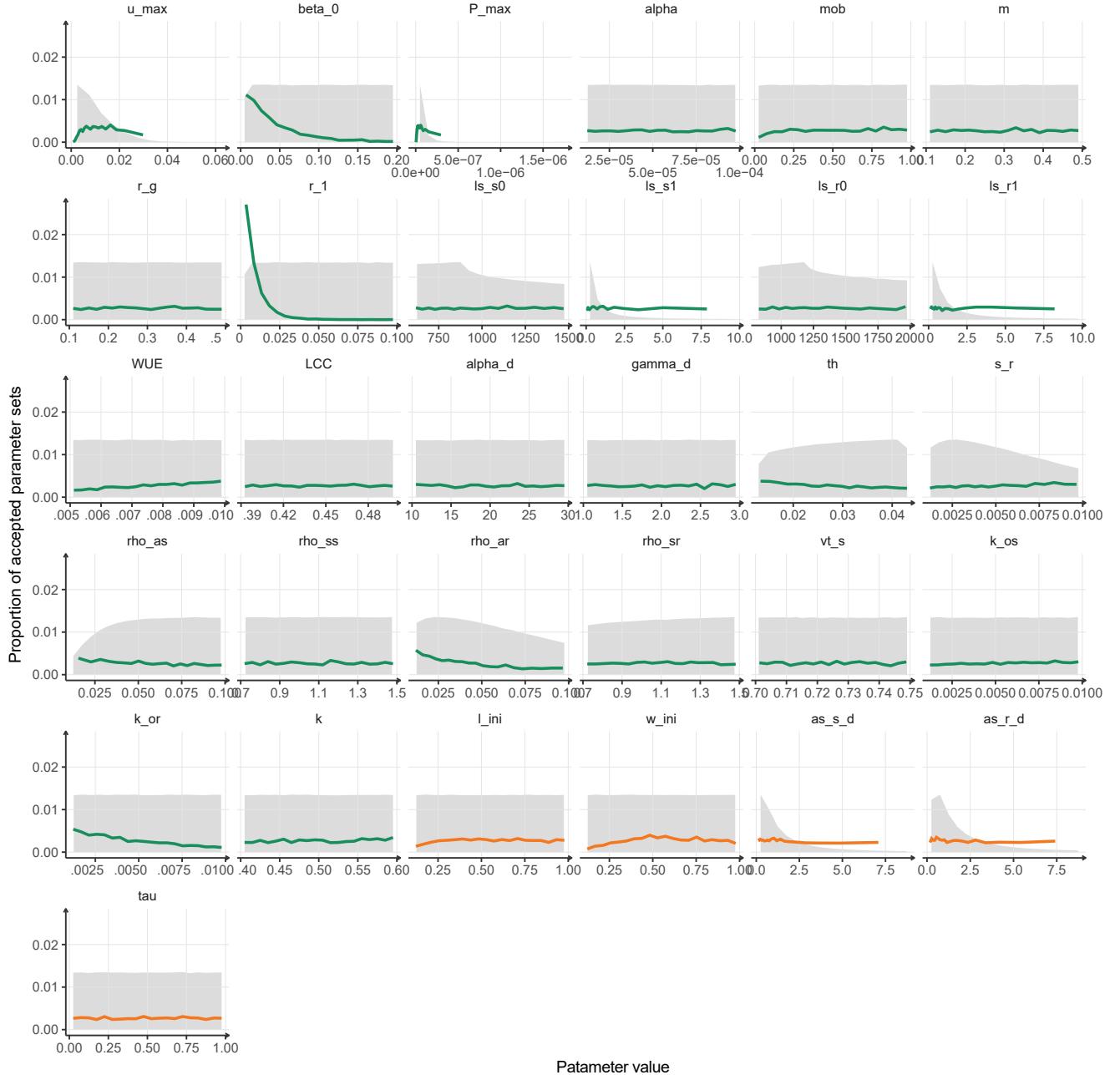
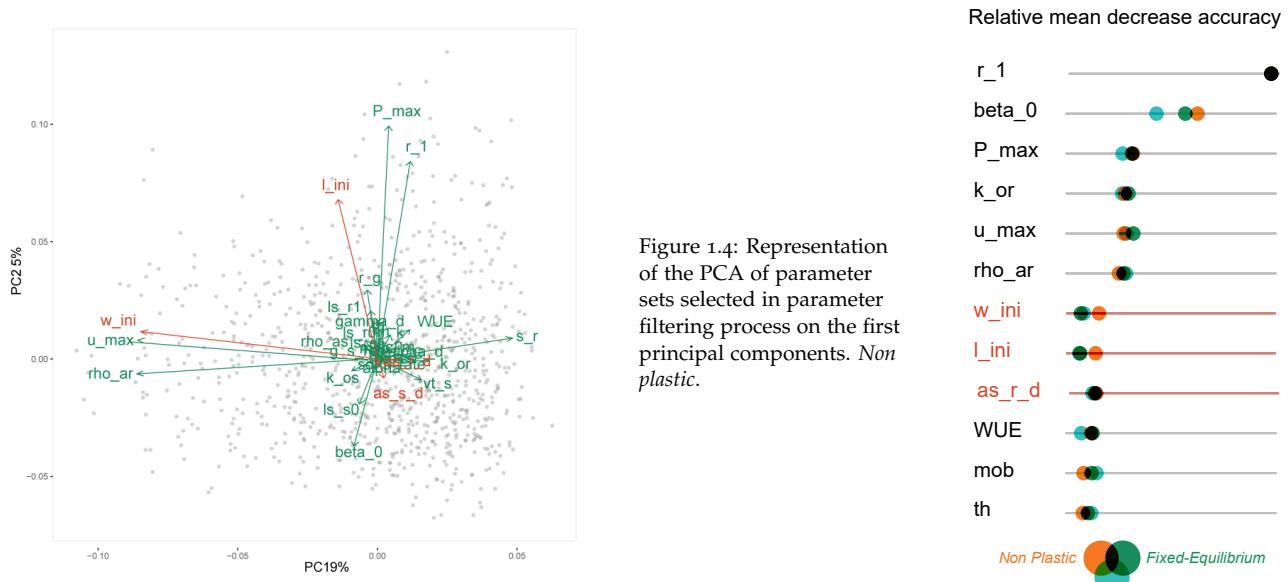


Figure 1.2: Selection rate (coloured lines) per parameter (global and species specific) for the individual growth. The grey area illustrates the prior distribution after the first filtering step (see the method paragraph for more details). Non plastic.



The PCA performed for *non plastic* algorithm only on parameter values reveals that the important parameters are also the dominant variables that shape the selected subspace. The two first axis explain only 14% of the variance. The first one is related to the root activity and efficiency (u_{\max} , l_{ini} , ρ_{ar} and s_r), the second is in line with global efficiency and resource availability.

The parameter filtering process is based on individual species, thus differences in the distribution of the accepted parameter sets are expected. Species can be distinguished neither on these two main component space, or on the species specific parameter space (l_{ini} , w_{ini} , w_{ini} & l_{ini} , as_{s_d} , as_{r_d} , as_{r_d} & as_{s_d}) despite small variations in distribution shapes and ranges between species (data not shown).

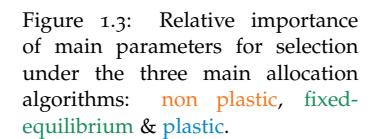
For each algorithm the response of the two filtering variables (weight and RSR) is plotted against the most important variables in figures 1.5 and 1.6.

VARIABLE RESPONSES

The total biomass is particularly sensitive to the tissue respiration cost (r_1), but also to the maximum exchange rate parameters. There is a notable difference in growth maxima between the two conditions in favour of the wet condition, in line with observed data. This difference is observed for the three algorithms that differ mainly by the amplitude of the biomass ranges (need data). Growth response curves are similar for all allocation algorithm. Growth is only weakly related to species-specific parameters. Total biomass under *Plastic-optimisation* algorithm seems to be more sensitive to variables influencing the exchange area per unit of biomass.

The species-specific parameter τ controlling the balance between genetic and environmental control does not emerge as an influencing parameter at the global scale for any of the two flexible allocation rules.

Root:Shoot Ratio (or RMF in figure 1.6) strongly responds to species-specific parameters under *non plastic* allocation because the memory parameters (l_{ini} and w_{ini}) are the means plants control their RSR. For other allocation rules, species-specific parameters have little control over RSR. Surprisingly, the photosynthetic capacity has a stronger influence on the ratio than the root maximum exchange rate.



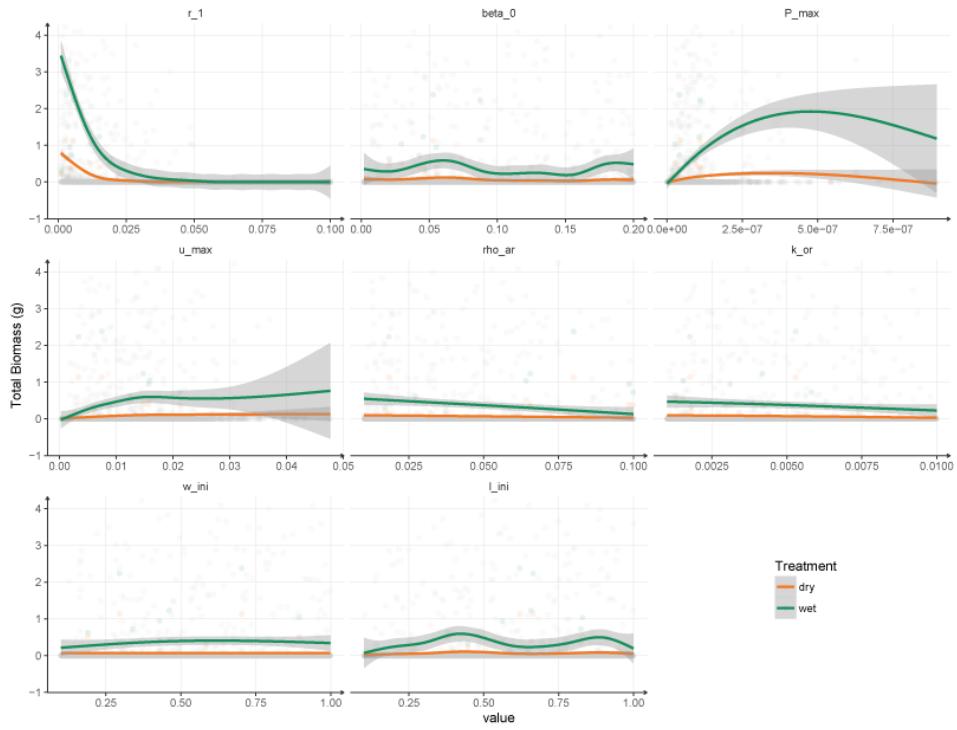


Figure 1.5: Main parameters effect on the total plant biomass. *Non plastic*. One dot represents a parameter set. Not all parameter set are represented as the y axis is limited around the smooth function (local regression). Coloured points represent selected parameter sets in the two treatments (**dry** and **wet**).

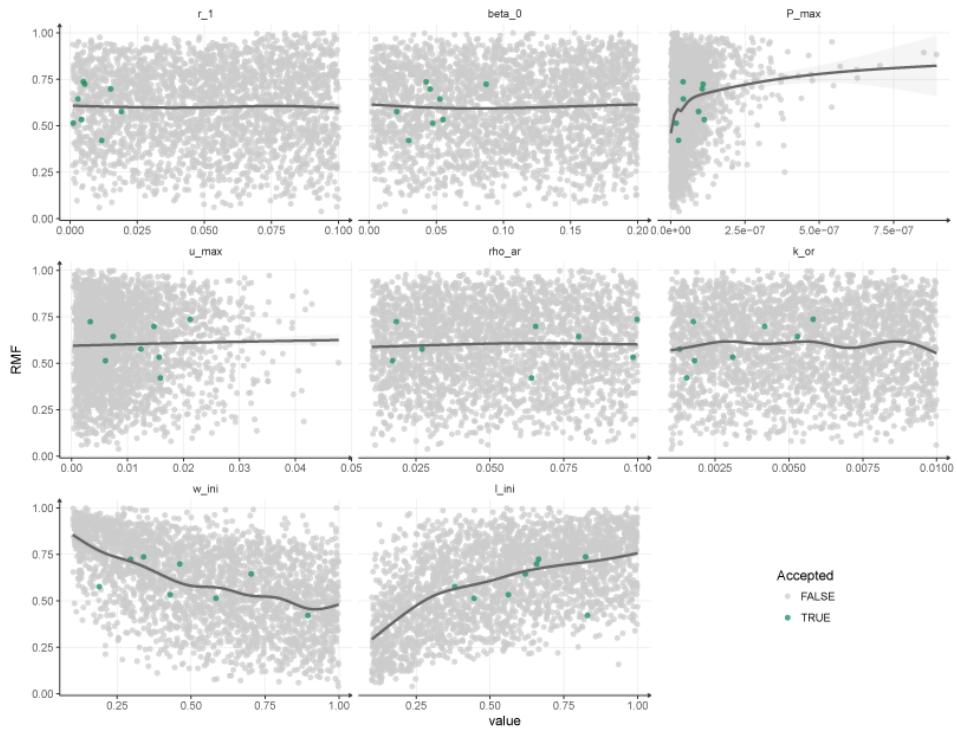


Figure 1.6: Main parameters effect on the total plant Root Mass Fraction (RMF). *Non plastic*

Little to no difference in RSR is expected for *non plastic* allocation rule since allocation promoted a fixed phenotype, but both *fixed-equilibrium* and *plastic-optimisation* allocation rules allow for changes in RSR. Nevertheless, no stable change in RSR is observed in any of the simulations. Fluctuations are present but consist in stable oscillations between two fixed values (see figure 1.7), synchronized with water variations. These rapid adaptations of the relative proportion of roots denote a high flexibility of plant phenotypes in *MountGrass*.

ROOT SHOOT RATIO AND PLASTICITY

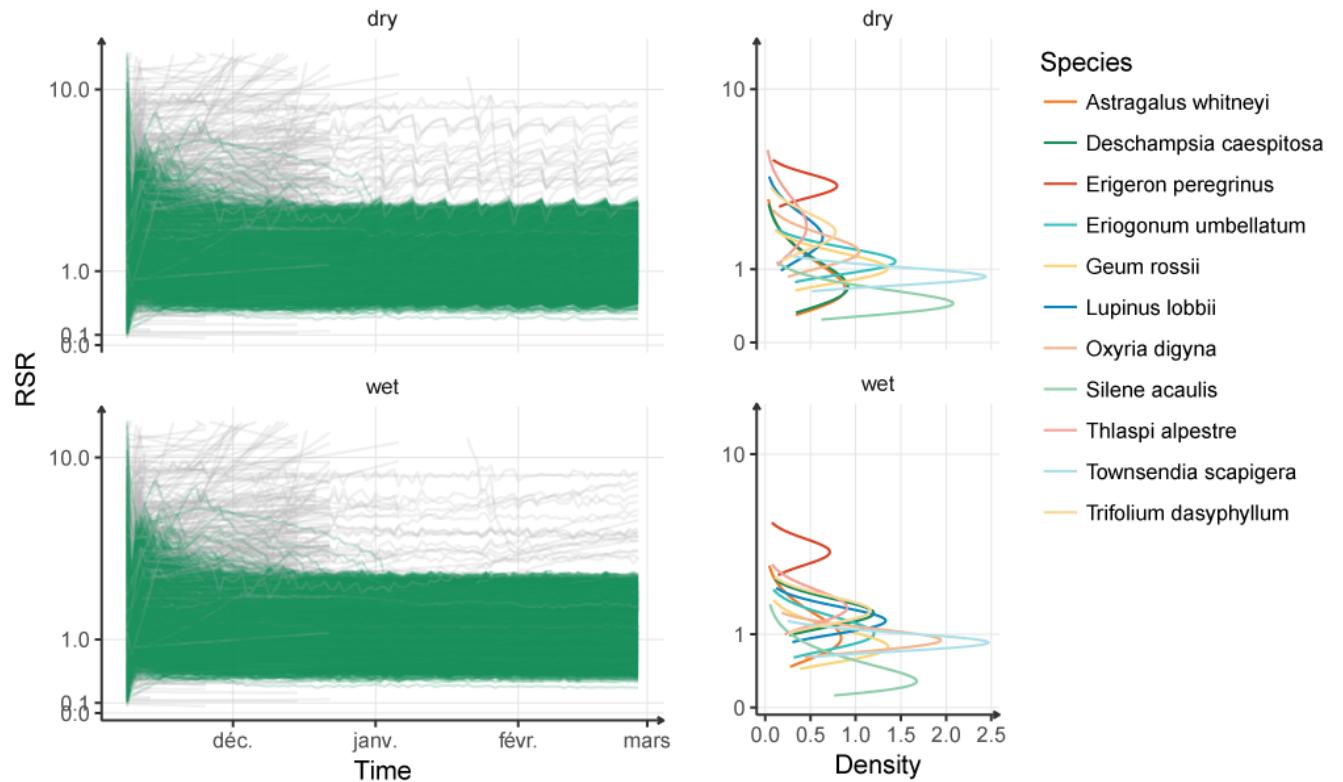


Figure 1.7: Comparison of simulated values of RSR with real species RSR in two contrasting conditions. Because there is no plasticity or ontogeny, the simulated plants do not express any changes in RSR. *Fixed-equilibrium*.

1.1.3 Discussion

The relative low selection rates for all allocation rules highlight the complexity of fitting such complex model to empirical data, despite the relative simplicity of the data. This difficulty seems to lie in two factors: the high number of parameters and the lack of stable changes in RSR. This last point is further discussed in the following paragraphs. Nevertheless, plant growth is reproduced in two contrasting conditions for multiple species. While plastic algorithms have a greater potential for growth (higher growth rate), this is not systematic and the absence of clear pattern for the most influencing parameters, such as maximum exchange rates and respiration rates, indicates that such high growth depends on a combination of parameter values. I believe that the shape of gain and cost functions along the functional trade-off between active and structural tissues plays a de-

GROWTH AND STRATEGY SPACE

termining role in the growth. A trade-off function with a wider viable range is more likely to be selected as more strategies would grow (therefore reducing the relative sensitivity to species-specific parameters). Considering the exponential shape of the turn-over function (one of the main cost with respiration), the width and height of the trade-off (or net gain function) is probably more strongly linked to the gain functions (exchange rates) and linear cost function (respiration), explaining little effect of parameters related to lifespan (already preselected otherwise). There is a strong dependency between viable strategies (and as a consequence of functional potential diversity) and the main trade-off between resource acquisition and efficiency.

Filtering the parameter sets based on all species instead of individually would have been ideal to quantify this link and better calibrate the model. However, such approach would have required many more simulations, when the parameter filtering method was chosen for its low computational cost. Moreover, considering the number of species-specific parameters, fitting the strategy subspace (at least default active tissue allocation parameters, the memory of resources and stability) of 11 species to the data in combination with more than 20 models parameters is near impossible. Ones should have had first determined the relative positions of the species within the said strategy space before any global calibration routine. Nonetheless, species-specific parameters have an influence on model main variables. The memory parameter affected the RSR in the context of *non plastic* allocation rule (see figures 1.7 and 1.1.2), while the default proportion of active tissues in roots was an influencing parameter in all algorithms (figure 1.1.2, `as_r_d`). Therefore, they should be analysed in further simulations within the same set of model parameters.

Because of the model complexity and the number of species-specific parameters, in addition to long simulation time, Bayesian calibration could not be performed. In the Bayesian paradigm, the information is contained in the data and revealed by the structure of the model. An alternative modelling approach is to use the parametrisation phase to accept certain parameter sets, and learn about the system through simulation experiments. The simulated data is analysed rather than empirical data. The patterns emerging from the simulation experiments inform us of the impact of the modelled mechanisms (even if they do not totally match the data). Therefore the model is still an understanding tool and can inform about the effect of plasticity on ecological processes.

The growth is reproduced in contrasted conditions, but only partially as one species per parameter set is tested. The number of species and dimensions in the strategy space would not allow for a calibration of all species for one parameter set. The plastic response of the root:shoot ratio is not correctly reproduced and would require a different implementation (stress based). However, the plasticity as implemented improved the acceptance rate because of a better growth. Therefore the effects of plasticity can still be investigated with simulation experiments.

If the parameter filtering step does not result in the selection of optimum values for all parameters, it provides information on the main mechanisms influence plant growth. Indeed, the relatively high importance of parameters related to water shows the importance of the resource on the model behaviour. Both water availability (water absorption limitation, exchange rate) and root mass and construction parameters are important to match the empirical data. Considering

that the calibration relies on experimental data of drought events, it is no surprise that parameters related to water economy show a strong influence on the selection rate and model behaviour. In the context where the model has been developed, water shortage is expected to be an important factor for the community dynamics. In this perspective, the ability of *MountGrassto* reproduce the differences in productivity between both conditions, and the relative sensitivity to water-related parameters is an advantage. The link between water resource, species strategy, plant performance and phenotypic plasticity is explored more in details in the following section.

The sensitivity of the different variables to the parameters align with the two criteria of selection (that work with the independence of trade-off). In contrast with forest, the light is not the most important factor and water plays a more limiting role. A particular focus on below-ground resources should drive the simulation experiments with this model.

As mentioned earlier in this discussion, the model is not able to produce any shift in RSR in different water treatment. It is not a surprise for *non plastic* algorithm, but the filter was still applied on this criterion to allow the comparison with the plastic algorithm and to be able to measure the improvement in selection rate. However, even plastic algorithms do not show strong enough response to water treatment in term of RSR. A strong and good (in the sense it would have matched the data) is larger in amplitude and more stable in time. Such processes generally amplify with time, *i.e.* when the number of drought event increases, the response (allocation to roots) increases (relative to default phenotype). Unlike natural systems, plants in *MountGrass* fluctuate between two 'states', or phenotypes associated with the dry and the wet conditions. The value of the RSR following a drought event is reached after the first week without water. This can be explained by two main mechanisms that are related but have contrasting implications. The quickness in response to the changing conditions is allowed by relatively high assimilation rates. While the net growth rate is limited by the comparison during the filtering process of the total weight of plants with the empirical data, the assimilation rate is not and can be compensated with a relatively high turn-over rate. Net growth rate being equal, species with higher assimilation rate will have higher **phenotypic flexibility** (higher fraction of biomass to invest in carbon pool of choice) than species with lower assimilation rate (but lower turn-over). This flexibility, similar to reallocation, allows changes in RSR, but not the accumulation of biomass in roots. Unfortunately, both the constant turn-over rate implemented in the model and the selection toward 'wide and high' gain functions limit control on this aspect.

This generalised high phenotypic flexibility, allowed by high assimilation rates to compensate high turn-over rates, highlights a problem within the calibration. The reproduction of growth patterns gives us confidence in the good functioning parameter filtering process, so wrong priors are certainly the cause of this behaviour. The uncertainty around the exchange rates for shoot and roots lead to the definition of relatively wide priors informed by parametrised models (Kleidon & Mooney, 2000; Reineking *et al.*, 2006; Taubert, 2014). In the other hand, the turn-over parameters are relatively well informed by modelling approaches but also empirical studies (Luke McCormack *et al.*, 2012; Ryser & Urbas, 2000; Tjoelker *et al.*, 2005; Wright *et al.*, 2004), leading to more constrained priors. The value of these priors is not discussed, it is rather how they are

PHENOTYPE FLEXIBILITY

translated within the context of the model leading to an over-estimation of the cost of leaf senescence. Because the lifespan is integrated at the daily time-step as a constant turn-over rate, instead of a late decrease in biomass as in natural systems, the biomass is reduced early in the growth (from day 0). This can be a problem when the growth is non-linear, especially when growth is higher early in the growth period. In this context, fairly narrow priors can lead to an over-estimation of the turn-over cost as the non-linear growth is not properly integrated by the integration of the tissue senescence. This over-estimation is then compensated, during the parameter filtering process by a higher assimilation rate and a higher tissue flexibility.

The particular design of the experiment from Peterson & Billings (1982) with cycling wet and drought periods can also explain this effect. Other experiment designs with shifts in the mean influx of water would limit the role of the phenotypic flexibility and show more consistent differences in RSR between wet and dry conditions.

Moreover, the fact that plants are more productive during periods where they may not want to invest in roots reduces the possibility for a strong durable shift of RSR. Indeed, a plant would drift to higher RSR if it was more productive when pursuing the high RSR phenotype than when pursuing the low RSR phenotype. This last point mentions the ‘will’ of the plant, in the context of *MountGrass* this target-phenotype is encoded in the projection of external conditions. Because this projection is daily based on design, the accumulation of drought stress is not translated in the internal projection variables of the plant (like it can be with the accumulation of phytohormones.). This limitation highlights a big difference between simulated plants in *MountGrass* and natural plants. While solutions to overcome this problem can easily be imagined (see equation 4.28 in 4.3.3), they would require more parameters and introduce more complexity to the analysis. This model provides a first approach to phenotypic plasticity in grassland models and the formulation of the projection, key element of the phenotypic plasticity, is certainly a starting point for further development. Nevertheless, the differences in response to the parameters between the three allocation rules, despite shared plant functioning, demonstrate the importance of plasticity itself. And simplification of the processes should not be a reason to not explore its effects. The fact that the parameter tau has a relatively small impact on selection rates also support the need to better understand all strategic axis before focusing on the effect of projection. While there are many ways of simulating the phenotypic plasticity, the parsimony is privileged. This simple representation is enough to understand the effects of active plastic allocation in association with the other strategic differences between species.

The high flexibility of the plant phenotype given by the high assimilation and turn-over rates reduces the inertia of the model and its capacity for modelling lasting changes in RSR. The modelling of the plastic response also reduces the capacity of the model to well capture changes in RSR.

The parameter filtering process successfully captures the growth pattern, showing convincing patterns of parameter sensitivity and variable response. However, limitations in the plastic response modelling, coupled with high phenotypic flexibility and a particular experiment-design do not allow a solid representation of the RSR differences between the conditions. Nevertheless,

the *MountGrass* still offers a way to interrogate the effect of plasticity on growth patterns, optimum strategies and potential diversity.

1.2 Individual level behaviour and properties of plastic allocation algorithm driven by the plant memory

Calibration and sensitivity analysis gives information on the main processes of plant growth, but the general effects of the allocation rules on plant growth are not fully identified. Moreover, because the parameter filtering processes were limited to individual plants and the effects of the species-specific parameters are depending on the other parameters of the model, the effects of these species-specific parameters should further be investigated. The objective of this part is to set better understanding of the role of the **allocation rules** and species **memory** on plant development as the basis for interpretation of plasticity effects in following chapters.

The challenge of the framework presented in the paragraph 2.2.1 under *plastic-optimisation* is to control the phenotype with the values of the memory. The risk of this approach is to have too tight estimation function of the fitness (or driving function) and to see the convergence of all species (with different memory values) toward the same phenotype (same allocation of active and structural tissues in roots and shoot). The extent to which different species memory lead to different phenotypes under full genetic control (not influenced by the external conditions) is explored through simulation experiment under *plastic optimisation* allocation algorithm with no effect of conditions on traits ($\tau = 1$), only on growth.

1.2.1 Method

The effect of allocation rule on phenotypic development is investigated thanks to pot simulations (see Methods in 1.1) of 100 days in 3 watering treatment: 2mm, 8mm and 16mm per day. To avoid drift in the phenotype due to allocation algorithm (see paragraph 2.2.1 on phenotypic determination), simulations were run a first time, then rerun with default specific traits matching traits at the end of the first simulation set. All four algorithms are simulated. To reduce the number of simulations 100 parameter sets are selected randomly within the accepted parameter sets for the *non plastic algorithm*.

ALLOCATION ALGORITHMS

The memory of external conditions plays a determining role in phenotypic development under *plastic-optimisation* allocation rules. The effect of the memory alone (environmental cues ignored by setting tau to 1) on the default emerging phenotype is explored for diverse memories (9 values on the two axis from 0.1 to 1 later scaled to the maximum area exchange rates for model parameter set considered, or 81 values) for each accepted parameter set. The effect of the memory values on the final position of plants in the phenotypic space is visualised by fitting loess curves between memory values and individual trait values.

MEMORY & PHENOTYPE

1.2.2 Results

The allocation algorithm affects the way the organic matter is distributed between the different tissues of the plant. With partitioning coefficient pre-established

ALLOCATION ALGORITHMS

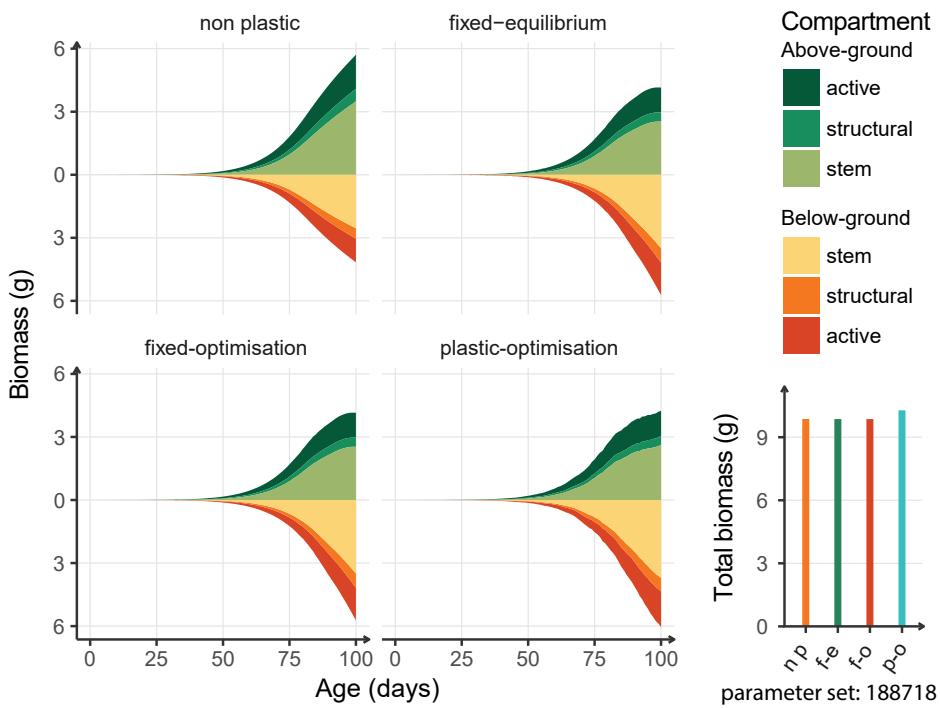


Figure 1.8: Effect of the different allocation algorithms on the different biomass compartments of the plant. The fraction of organic matter allocated to the stem (ensemble of supporting tissues for shoot and roots) are increasing over time for all algorithms. The *non plastic* algorithm show constant allocation coefficients between above-ground and below-ground compartments and between active and structural tissues. All others show different coefficients for the above-ground - below-ground partitioning, and the *plastic-optimisation* algorithm have changing proportion of active and structural tissues. The bottom-right panel shows the total biomass for the four allocation algorithms after 100 days.

for the given conditions, the algorithm shows very similar performances (see figure 1.8). The difference in allocation algorithm is mostly noticeable in figure 1.8 mostly on the shift toward root allocation at the end of the simulation when the water starts to be limiting. The plant under *plastic-optimisation* allocation benefit from a slight improvement in performance (mean: +10%, median: +3.4% relative to *non plastic*).

The *plastic-optimisation* algorithm allows changes in the proportion of active tissues in organs. This may have repercussions on the allocation between shoot and root but also can lead to non-specific variability within plants with no perception of resource fluctuations ($\tau\alpha = 1$). The median variability of the RMF (root mass fraction) along the 100 simulated days is 0.015, that is five times higher than the variability of the other plastic algorithms (*fixed-optimisation* and *fixed-equilibrium*) (see table 1.4). This variability is much higher (around 0.028) for the plastic plants in all three plastic algorithms, while it is null for the *non plastic* allocation rule. The range of the RMF follows a similar trend, with a higher value for the *plastic-optimisation* than the other algorithms when plants do not perceive the resource fluctuations, and wide range for all plastic allocation algorithms when plants take into account the changes in light and water resources.

algorithm	sd		range	
	tau = 0	tau = 1	tau = 0	tau = 1
none	< 10^{-12}	< 10^{-12}	< 10^{-12}	< 10^{-12}
fixed-equilibrium	0.0278	0.00212	0.173	0.0155
fixed-optimisation	0.0279	0.00221	0.173	0.0161
plastic-optimisation	0.0283	0.0150	0.174	0.0839

Table 1.4: Median of variability and range of the RMF for simulations of 100 days, for 100 different parameter sets and three different water treatments (2, 4 and 8 mm per day), in the four different allocation algorithms. sd: standard deviation.

The plastic algorithms show similar levels of variation and range, while the *non plastic* one is stable as expected. The *plastic-optimisation* allocation show more

instability for non plastic plants ($\tau = 1$) but that is lower than the variability observed in plastic plants ($\tau = 0$). The allocation (and therefore phenotype) is controlled by the allocation rules (plastic dimensions and objective functions) and the estimation of conditions. Before investigating the effects of varying conditions, it is important to understand the effect of memory on plant strategy and phenotype.

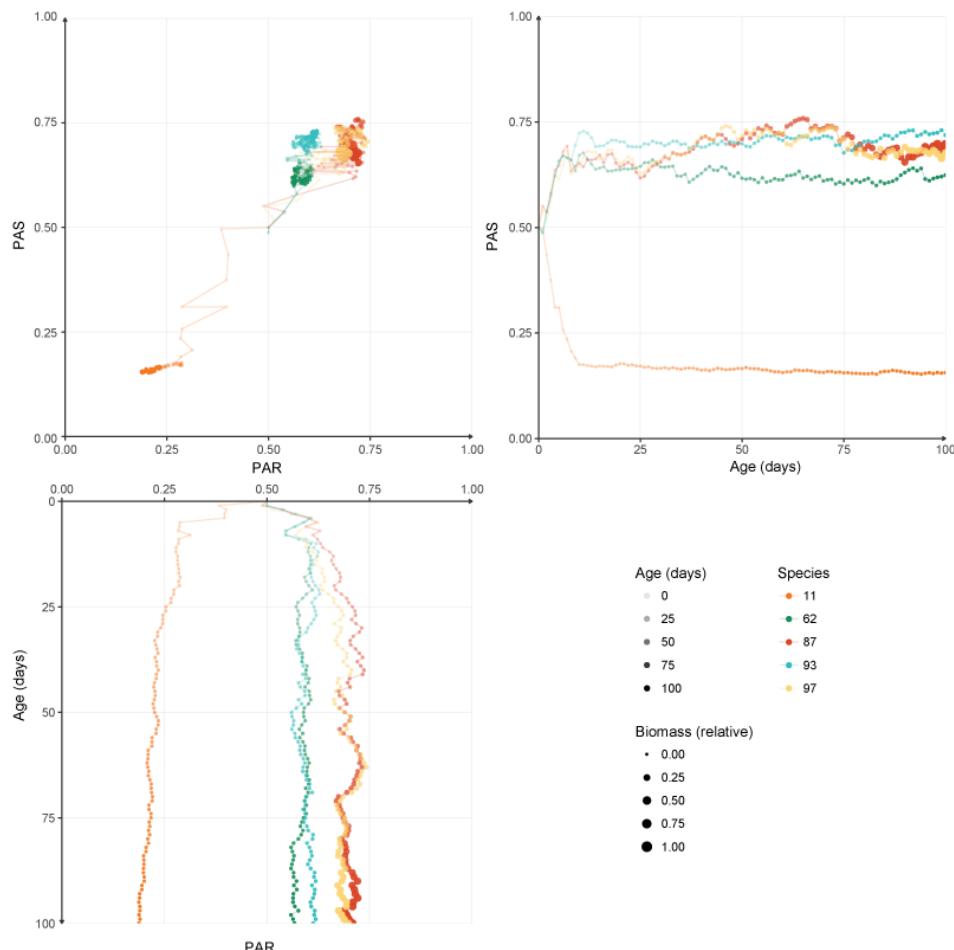


Figure 1.9: Trajectories along time in the strategy space of 5 plants with different memories. After 10 days, all plants have converged toward the estimated optimum.

The kinetics of the phenotypic shift is first visualised for one parameter set on the two main phenotypic axes (proportion of active tissues in roots: PAR and proportion of active tissues in the shoot: PAS). From the same starting point, the five species show a distinct rapid shift toward segregated subspaces of the 2D strategy space. The equilibrium point is reached in approximately 10 days for all 5 species. Despite constant memory, variations are visible on both tissue allocation traits of roots and shoot. These variations lead to partial overlap but the five species are distinct on the 2D space.

MEMORY AND PHENOTYPE

The memory of resource availability is a strong enough driver to alter the default phenotype of a species. The effect of the two components of the memory (memory of water availability and memory of light availability) on the three main traits is explored through local regressions. The proportion of active tissues in roots increases to a plateau with the increase in water availability memory (figure 1.10). This response pattern is consistent between all parameter sets, but

the starting points and slopes may differ. The same pattern is observed between light availability memory and proportion of active tissues in roots (data not shown). The allocation convergence in the root is also influenced by the increase in light availability memory. An increase in the latter leads to a smooth increase in the former (see figure 1.11) with less drastic response than the water. This response is mirrored in shoot allocation response to increase in water availability memory (data not shown). Both organs react in symmetric ways to increase in resource availability. The RSR has a negative log response to water availability memory (positive in the case of light availability memory).

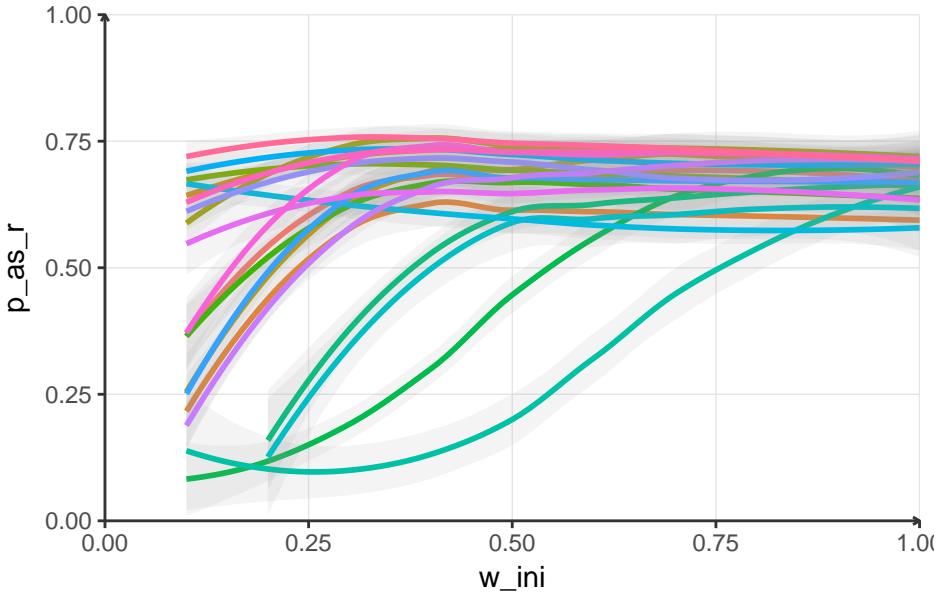


Figure 1.10: Effect of memory of water availability on proportion of active tissues in roots. *Plastic-optimisation*. Each line correspond to a local regression fitted for all memory combinations for a given parameter set. Water availability memory is given in percentage of maximum exchange rate, absolute values may change between parameter sets.

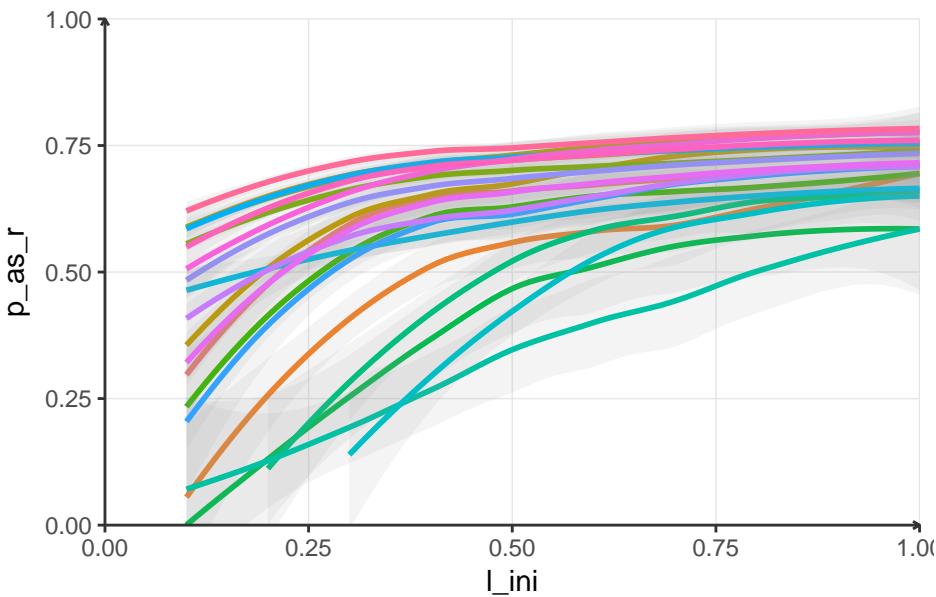


Figure 1.11: Effect of memory of water availability on proportion of active tissues in shoot. *Plastic-optimisation*. Each line correspond to a local regression fitted for all memory combinations for a given parameter set. Light availability memory is given in percentage of maximum exchange rate, absolute values may change between parameter sets.

The combined effect of the two axes of plant resource availability memory is observed by plotting the phenotypes (on the 2D space of active tissue allo-

cation) of four contrasting memories for all parameter sets (figure 1.12). There is clear clustering of the four memory profiles, with some overlaps due to the fact that multiple parameter sets are plotted at the same time. The memory of low availability (●) has a much larger distribution area than others, suggesting the relative instability of this profile within the "estimated net gain landscape". A memory of low availability for both resources drives plant toward very conservative strategies than other strategies. High expected availability of at least one resource increases allocation to active tissues to both organs. This confirms the positive effect of complementary resources (light for roots and water for the shoot) of active tissue allocation in organs (see figure 1.11). Because of this, there is no highly unbalance phenotypes with high contrast between organ-specific allocation emerging from the *plastic-optimisation* allocation in *MountGrass*. There is general coordination, but the balance between resource availability memories still impacts the position on the 2D, illustrated by the absence of overlap between low light - high water (●) and high light - low water (○) phenotypes. In case of high resource availability and coordination, high investment in active tissues for both organ is achieved (●) and high light - high water), but the range of values is similar than for unbalanced memories (●) and high light - low water (○).

1.2.3 Discussion

The pre-calculation of phenotypes, avoiding any phenotypic drift, allows for all allocation rules to grow plants with close performances. Nevertheless, the plastic algorithms show changes in RMF at the end of the simulation when the light:water balance starts to shift. This consistent shift in RMF for all three plastic allocation rules (with a low variation of the other plastic dimensions) suggests the sensitivity and importance of this phenotypic axis. On the other hand, the other plastic dimensions benefit the plant growth suggesting that they also play a role in the tissue efficiency. While both the RMF and the proportion of active tissues can change the exchange area, only the proportion of active tissues can change the tissue efficiencies. Because the RMF shows similar levels of variation and range in both *fixed* algorithms (RMF is the only plastic dimension) and *plastic-optimisation* algorithm (see table 1.4) the allocation of active tissue in the latter algorithm does not compensate for change in root:shoot allocation and is not used to increase the area of the limiting organ. This is confirmed by the fact that memory of low-light conditions (● in figure 1.12) lead to lower allocation to active tissues than high light conditions (○). In the case of fully plastic plants trying to optimise their growth, the vegetative phenotypic dimensions do not fulfil the same functions: the RMF is used to adjust the balance between the resource exchanges while the changes in active tissue proportions are related to the tissue and whole plant efficiency. This contrast in functions looks opposed to what is often observed in empirical studies where shoot:root ratio and SLA (here controlled by the proportion of active tissues) respond in the same direction to increase the leaf area and compensate low incident light (Poorter, Niinemets, *et al.*, 2009; Poorter, Niklas, *et al.*, 2012; Ryser & Eek, 2000). This discrepancy reveals a limitation within the plastic-allocation algorithm: the balance function is mostly supported by changes in root:shoot ratio while the proportion of active tissues (controlling SLA and SRL) controls the tissues efficiency. The low proportion of active tissues in low resource (● in figure 1.12) indicates a

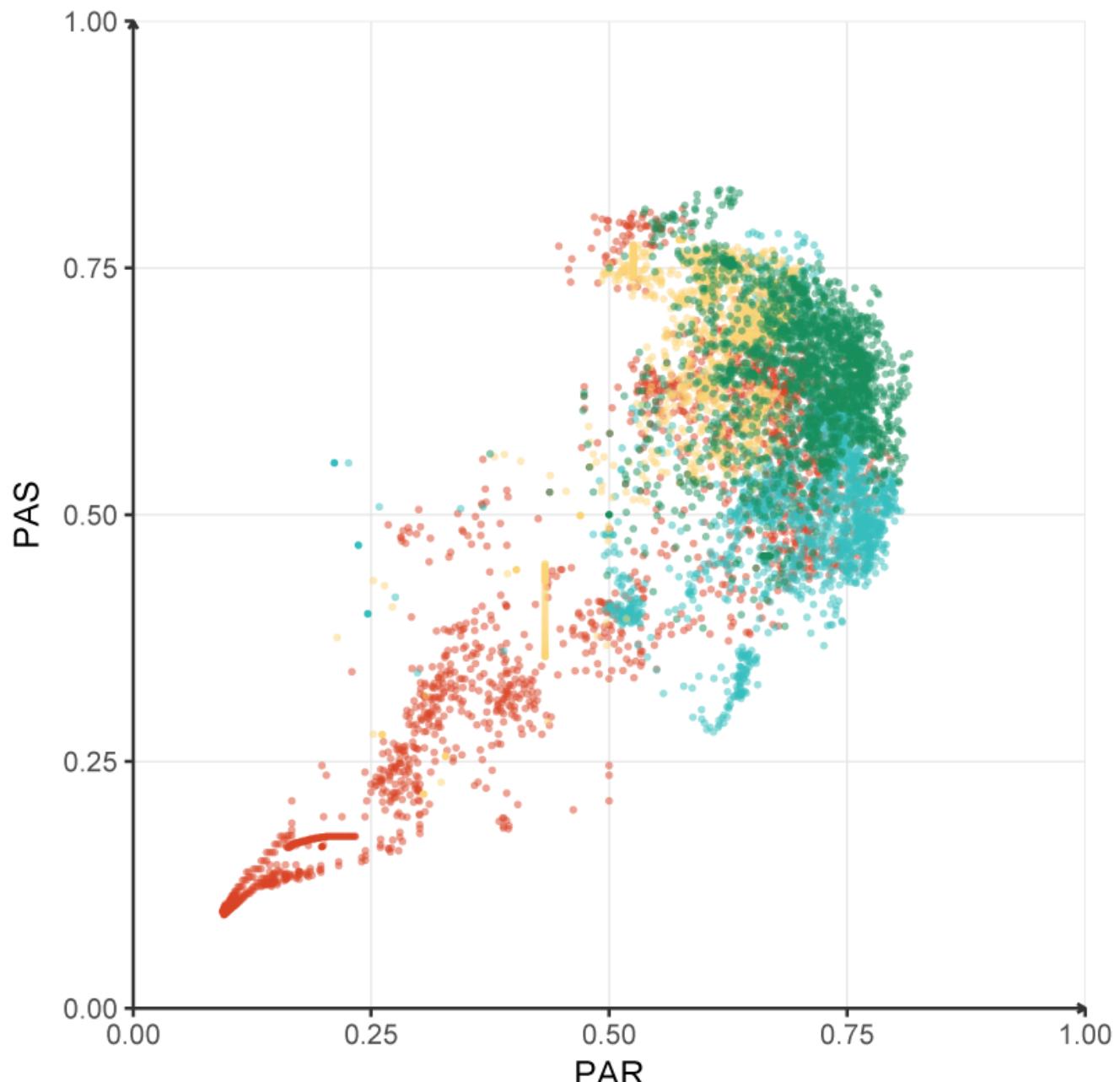


Figure 1.12: Impact of species memory on final phenotype in case of fully plastic allocation. *Plastic-optimisation*. Each point corresponds to a plant phenotype for a memory syndrome for a given parameter set. Colours denote the memory syndromes.

- low light - low water,
- HIGH light - low water,
- low light - HIGH water,
- HIGH light - HIGH water.

selection of more conservative phenotypes when the resource is scarcer. This is in agreement with the Grime's triangle (Grime, 1977) and large-scale empirical studies (Wright *et al.*, 2004). In contrast with the conclusions of Ryser & Eek (2000), here the full phenotypic plasticity of the *plastic-optimisation* algorithm is driven by similar constraints than the long-term selection processes. This can be explained by the design of the trade-offs that drive the gain function (see chapter III). Therefore there are strong constraints on the tissue allocation, but low constraints on the root-shoot allocation. An additional constraint of this dimension can be added by considering other functions of each organ (such as nitrogen absorption by roots), or more artificially by increasing the cost of the displacement along the RMF axis. The fact that traits and allocation may be constrained in different ways has been observed by Freschet, Swart, *et al.* (2015), highlighting contrasted types of response between shoot and roots (Poorter & Ryser, 2015). Also, it appears here that studying the long-term effect of a fixed estimation of conditions is probably not the best way to understand how the plastic responses of plants to an abrupt change in conditions. However, in *MountGrass*, the plasticity is driven by the same mechanism, so such interpretations can be made. But, this discrepancy suggests that mean phenotype and plastic responses should probably not be driven by exactly the same mechanisms.

In addition to this imbalance in constraints, the mean organ approach can also explain this behaviour. Approximating the properties of the canopy by considering one mean organ leads to a low impact of the plastic allocation on the SLA and SRL if the already existing compartments are large relative to the growth, a high importance of old tissues, while most of the exchange activity is generally produced by freshly grown tissues. Also, the rapid growth and turn-over in numerous parameter sets also authorise rapid plastic response on the RMF dimension (see also the rapid oscillations in the figure 1.7 top left panel), diminishing the need for tissue-specific adjustments. A stronger calibration of gross production and turn-over rates, as mentioned in the previous section, should reduce this effect. Finally, the optimisation function may be too strong and plants may not always go for the optimum allocation but for the fastest and most competitive choice (see Dybzinski *et al.* (2011) and Farior (2011, 2014)). If this is not a problem in the context of this simulation where the memory is used to drive the default phenotype of the plant, it would be problematic in the context of plastic responses.

The different allocation algorithms impact the vegetative phenotype in different ways, but with a similar performance when any phenotypic drift is avoided. But, the plasticity along the three main dimensions of the plant vegetative phenotype (PAR, PAS & RMF) seems to have different objectives. While the RMF is the main adjustment variable to respond to changes in equilibrium, the proportion of active tissues is more closely related to the amount of resources and tissue efficiency. However, it does not reproduce increases in organ area by changes in traits when the related resource is limiting. Multiple factors can explain this partial discrepancy with empirical results. The model can still be used to better understand the role of the memory as a driver for the phenotypic development, and the effects of the plasticity (particularly the RMF dimension) on plant performances.

The *plastic-optimisation* allocation algorithm allows for interesting insights into how the different resources affect the theoretical optimum phenotype. The in-

crease in resource levels leads to an increase in the allocation of organic matter to the active tissues. While this is commonly demonstrated, the indirect effect of one resource on an organ that is not limiting for this resource is less often studied. A higher perceived resource availability drives plants to have a higher proportion of active tissues in both gathering (*i.e.* leaves for an increase in light availability) and other organs (*i.e.* roots for an increase in light availability). The direct effect on the related organ shows a rapid shift from low to a maximum value. This rapid shift can be explained by the fact that the increased resource availability both increases the slope of the exchange rate per biomass (gain function) and reduce the importance of the maintenance costs relative to the productivity, favouring the exploitative strategies.

In the other hand, the indirect effect of an increased resource level on the non-gathering organ can be explained by two mechanisms: a shift in the limiting organ requiring an increase in the exchange area of the newly limiting organ or an increasing gross productivity reducing the need for efficient organs. The former mechanism is related to the equilibrium maintenance. The balance between the two organs can be maintained by increasing the exchange area of the newly limiting organ (or reducing the exchange area of the non-limiting organ, see Liu & Stützel (2004) for an example, or Grassein *et al.* (2010)). However this type of response is unlikely considering this implementation of phenotypic plasticity. The changes in exchange area are mostly driven by the organ biomass rather than its proportion of active tissues (see previous paragraph). The latter mechanism is more in line with the observations of the behaviour of *MountGrass* (figures 1.12 & 1.11). It explains the increase in active tissues in both organs by an increase in the exchange rate of the gathering organ and in the productivity at the plant scale, decreasing the relative importance of maintenance costs and allowing for a more exploitative strategy of the organs.

Such allocation pattern could explain coordination between organs, as the cost of the respiration and turn-over are compensated globally by the gross productivity, and allows divergence from the optimum of the isolated organ functioning (see chapter III for details on the trade-offs at the organ's scale). However, this coordination along a fast-slow axis asks the question of the stability of this strategy. Indeed, the high investment in active tissues observed suggests that the turn-over and respiration costs are high, and a loss in efficiency based on an incorrect estimation of conditions could have strong negative effects.

The allocation trade-off allows for strategies from the fast-slow spectrum to arise for the shoot and roots based on the perceived condition availabilities with some degrees of coordination, in a coherent framework. Such allocation mechanism can explain coordination thanks to shared cost and increase efficiency when the resource is available. The potential instability of the phenotypes may lead to discrepancies between the optimum defined by the plastic-optimisation algorithm and the realised performance landscape.

The model *MountGrass* brings a new approach to agent-based models and plasticity by integrating the resource availability estimation directly as a parameter for the plant development strategy. Despite requiring certain adjustment for an integration with full plasticity (in RMF and organ-specific traits), it reproduces a certain pattern of coordination and overall resource use strategy along resource gradients. It also makes a bridge between the mechanistic approaches, that use species-specific parameters measure on individual plants and species

THE MEMORY CONCEPT

distribution models (SDMs) that focus on abiotic conditions¹ and how species distribution match climatic variables. This new framework can allow more exploration at bigger scales with numerous species, that is often the limitations of such agent-based models. However, to make this step, further work is needed on the general assumption that the estimation of conditions coupled with the gain function gives a good proxy to the plant development. There must be a strong positive correlation between the memory, the developed phenotype and the plant performance.

While this verification seems obvious, difficulties can arise if you consider plant with different levels of plasticity. A non plastic plant will certainly require the same memory as a plastic plant that will be able to adjust this memory. The former should conciliate the memory (and therefore the phenotype) matching the conditions of it growing period with values that limit risks of negative growth outside this favourable period. A mean value of the experienced condition during the growing period is certainly a good value for the memory. This also raises the question of the ontogeny in these models that often consider fixed allocation parameters. In *MountGrass*, ontogenetic shifts can be mimic under *plastic-optimisation* by having default allocation parameters different from the ones computed by the optimisation algorithm². On the other hand, plastic plants should better have a memory that matches the conditions at the early stages of growth, and let the plasticity drive the allocation for the continuation of the development. Also, while the structure of the model lets a door open for the integration of heritability mechanisms (through epigenetic modifications) that are expected to play an important role in the adaptation to the global change, those differences between plastic and non plastic plants may impact the integration of plasticity. This argument also encourages to find alternative solution to model plastic traits. Based on the review by Crisp *et al.* (2016), the concept of memory can be conserved but adapted to be more driven by stress levels and stress response/recovery than actual resource availability values. The knowledge of molecular mechanisms of the plant functioning must better inform the modelling routine that is too focused on mathematical and theoretical approaches. The advantage of such specific memory mechanism is that it can be stress specific³ and allows the integration of heritability.

The concept of memory, even if it allows the contrasting phenotype in a continuous space, should take a different form to suit multiple plasticity strategies and integrate a form of heritability. The molecular mechanisms of plastic responses are better understood and provide solid foundations for new organ-specific plasticity.

The model *MountGrass* integrates trade-offs in resource use driven by the memory in resource availability. The investigation of the allocation patterns driven by the *plastic-optimisation* algorithm under the assumption of maximisation of the daily growth demonstrates different roles of the phenotypic axes: the RMF largely controls the equilibrium between shoot and root total activities, while the proportion of active tissues are related to the tissue efficiency as well as the overall plant efficiency and resource use strategy. While the fast-slow gradient along resource gradients is reproduced, and organ partial coordination explained, plastic responses to answer quick changes in resources are likely to not be reproduced due to a lack of constraints on the RMF dimension. The effect of the different algorithm, plasticity strategy and

¹ new SDMs now integrate biotic interactions as well as other ecological processes, as suggested by Guisan & Thuiller (2005).

² limited here by a first simulation cycle, see methods for details.

³ as suggested in the chapter III.

resources affect the plant performance still have to be investigated. Despite the pieces of evidence that the *plastic-optimisation* allocation mechanisms needs adjustments, the *fixed-equilibrium* algorithm offer a great tool to study the effect of plasticity on plant performances and best strategies.

2 INDIVIDUAL PERFORMANCE, PLASTICITY AND VARIABLE CONDITIONS

The previous section highlighted the ability of the model to model growth, but also the importance of species-specific parameters. While the plasticity mechanism did not replicate to a full extent (stable and higher amplitude) the phenotypic changes between the different conditions, there were some changes both in traits and in growth, leading to a higher parameter set selection rate. Considering the importance of species-specific parameters and their potential impact on growth, these differences between plastic and non plastic allocation rules should be investigated in an extended manner. The specific roles of strategy and memory on the multiple components of plant growth need to be disentangled to draw better hypotheses on the role of phenotypic plasticity on plant performance and coexistence. The role of resource availability on these mechanisms also needs to be interrogated. The effect of plasticity on coexistence can also be approached with respect to relative performances and contraction of the strategy space.

This chapter tends to answer these questions with simulations of individual plants with diverse strategies and under multiple allocation rules. To simplify the approach and focus on the interaction between species strategies and allocation algorithm, the plasticity will be modelled as a discrete mechanism ($\tau = 0$ for all plastic allocation algorithms).

2.1 Individual performance: between strategy, memory and plasticity

This first subsection focuses on the link between the phenotype and the plant performance. The plasticity and allocation mechanisms can affect both the link between phenotype and performance and the distribution of the existing phenotypes.

2.1.1 Method

Because little differences are found between accepted parameter sets for the three main algorithms, parameter sets selected for the *non plastic* algorithm are used for all algorithm. To reduce the number of simulations but have a measure of the genericity of the observed patterns, 20 parameter sets are selected among the

PARAMETER SETS

accepted parameter sets for the *non plastic* allocation algorithm. As mentioned in the previous section, the parameter sets have been selected for only one species-specific and therefore an additional step was used to filter out the parameter sets that could lead to high biomass values. For each parameter set, simulations of diverse phenotypes run for 100 days of 15 hours with favourable temperature conditions (20 °C) along resource availability gradient. The parameter sets are selected based on the maximum biomass of all simulated plants. One parameter set is randomly selected for each of the 20 brackets between 0 and 2 grams of total biomass.

To better understand what makes a plant perform in the model require the growth of a multitude of phenotypes. Tested phenotypes are distributed regularly along the three axes of the strategy space (proportion of active tissues in root, proportion of active tissues in shoot, proportion of roots) between extreme values (respectively (0.1, 0.99), (0.1, 0.99) and (0.1, 0.9)) for a total of 3375 combinations (15^3). Because the RSR is defined by the memory, and in this set of simulation experiments the RSR is defined before, the species memory needs to be computed afterwards. There is an infinite number of couples of memory values that can match a given RSR. Also, the projection of conditions is sensitive to both memory and experienced conditions, therefore the choice of memory can affect the relative sensitivity of species to changes in external conditions and alter the model behaviour. Because the role of memory is not the focus here, and because there is interest¹ on the role of the plasticity as a mechanism (as opposed as a strategy with various values of tau), the parameter tau is set to 0. This ensures that only the starting phenotype and the experienced conditions play a role in plant performance.

For each phenotype a pot simulation is ran for 100 days of 15 hours under 4 millimetres rainfall and 120 Watt per square metres and per hour with the 4 main allocation algorithms (*non plastic*, *fixed-equilibrium*, *fixed-optimisation* and *plastic-optimisation*). Two resource levels are tested for each simulation. The low resource availability conditions correspond to a reduction by a factor 4 of resource influx, but the day length was conserved.

To visualise the performance landscape (plant performance relative to biggest plant as a function of its phenotype) the performance of best phenotypes are projected against the 3 plans that compose the phenotypic space. Such projections are preferred to 3D alternatives as they work better with static visualisation and when most of the space is occupied. Alternative axes are defined to facilitate the interpretation and description of the performance landscape: the organ strategy plane (PAR-PAS plane) can be transformed into strategy balance (differences between PAS and PAR) and "speed" (in sense of Reich (Reich, 2014))(the average allocation to active tissues).

To study the potential effect of resource availability and or allocation mechanism on the link between strategy and performance, an aggregated measure is designed: the **gravity centre** of the phenotypic space is defined as the average phenotype weighted by the relative performance of each phenotype. It can be defined with respect to the initial strategy, or to take into account the plasticity, to the final position in the phenotypic space. The shift of this gravity centre within the projection space informs of translation of the performance landscape.

STRATEGY SPACE SAMPLING

¹ at this stage of the exploration of the model

SIMULATION SET-UP

PROJECTIONS

Biomass measures are relative to best performing non plastic plant (to remove the general parameter set effect on growth) and compare (within each condition) the effect of allocation algorithm.

NORMALISATION

2.1.2 Results

The effects of the species-specific parameters on growth are first studied with the analysis of the performance landscape drawn by the growth of plants uniformly distributed in the strategy space.

PERFORMANCE LANDSCAPE

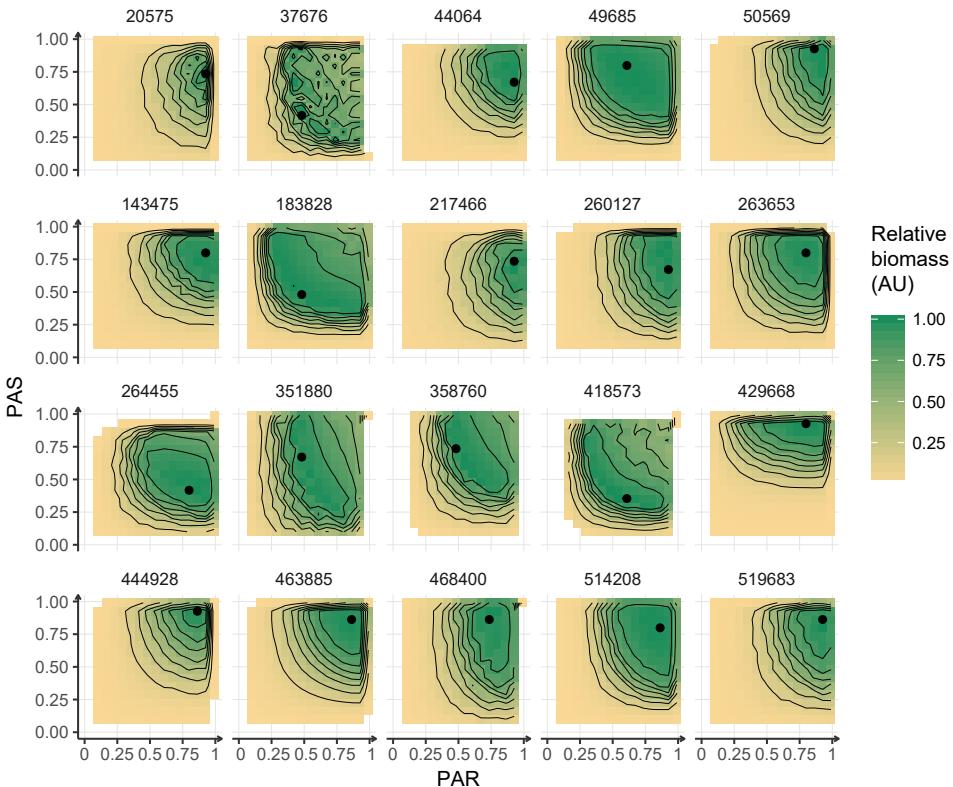


Figure 2.1: Projection of best phenotypes (varying RMF) on the 2D PAR-PAS plane for each parameter set. Points identify the optima. Non plastic.

On the tissue allocation plan (proportion of active tissues in leaves and roots) (see figure 2.1), the best performing phenotypes present a bean shape. This shape covers a good fraction of the space, in the centre and sometimes top-right corner (high active tissue allocation) of the 2D space, while other corners are ignored. Too low values for any of the organs lead to a limited growth. For certain parameter sets, the top-right corner, corresponding to high resource acquisition strategies, has lower growth values than the centre. They have lower growth values than phenotypes with similar values for one of the organs and a lower value for the other organ.

Projection of the best phenotypes over the three planes also gives information on the importance of the ignored variable on each plane. If the contrast between the growth projected phenotypes is high, at least on the main dimension is crucial for the growth. If the contrast is lower when the variable is ignored (*i.e.* the best value is used) then the projected variable is likely to be important. The projection on PAR-RMF and PAS-RMF (see figure 2.7) planes shows a higher contrast between phenotypes relatively to PAR-PAS plane, therefore the RMF is

a more sensitive variable than the allocation factors to active tissues in organs.

Introducing resource availability variations and plasticity can impact the shape of the performance landscape.

OPTIMUM SHIFTING

A shift of gravity centres can be observed between the two resource levels in all allocation algorithms (see figure 2.2, the four panels). *Non plastic* and *fixed* algorithm show similar trends with an increase in the proportion of active tissues in both organs. This change toward more exploitative tissues is consistent and can be observed for all parameter sets but one. The *plastic-optimisation* algorithm show drastically different responses of the gravity centre of phenotypes. There is little change in shoot proportion of active tissues, but a consistent reduction of active tissues in the root system, and a reduction of root mass fraction (data not shown). These two responses indicate a net reduction of root activity in favour of shoot activity. Two things must be taken into consideration while looking at these results: (1) the gravity center is computed from final position into the phenotypic space, not the starting position, (2) because *plastic-optimisation* algorithm allows changes in traits that are represented (PAR and PAS), shifts along these axes can be driven by the plasticity mechanisms and not necessarily only performance differences. A similar representation of the gravity centre computed from the initial phenotype (not shown) shows a similar response for the three first algorithms and no apparent shift for the *plastic-optimisation* plasticity.

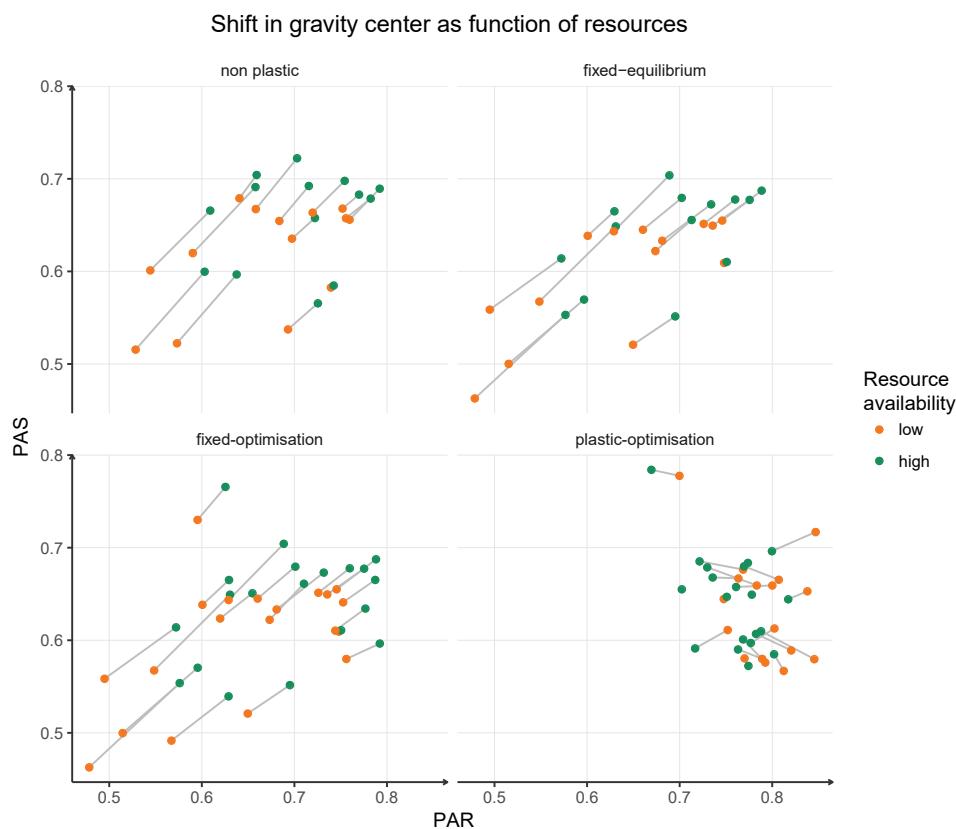


Figure 2.2: Shift on the 2D phenotypic space of the center of gravity as function of resource availability. The center of gravity is defined as the average phenotype weighted by the relative biomass, and characterises the performance landscape.

Non plastic and *fixed* plasticities respond in a same way to a shift in resource availability. However, we can note that the gravity centres have a lower proportion of active tissues for *fixed* allocation algorithm compared to the *non plastic* one.

Plastic allocation leads to an improvement in mean biomass of all individuals for all three plastic allocation algorithms (see figure 2.3). The *fixed-equilibrium* plants are 2.5 times bigger in average than *non plastic* plants (in low resource conditions), and up to 7 times bigger for *plastic-optimisation* plant. These ratios are relatively similar for high resource availability.

PRODUCTIVITY CHANGES

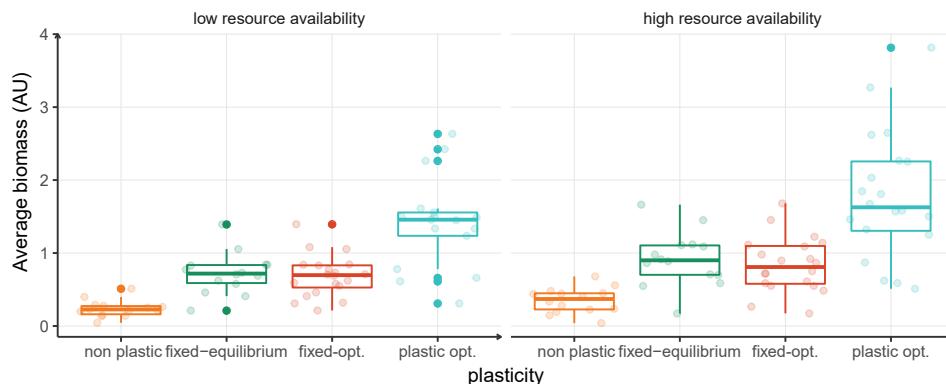
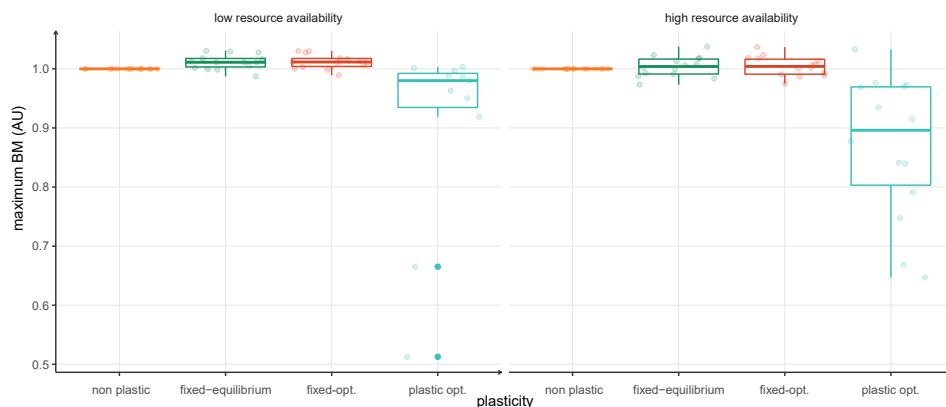


Figure 2.3: Mean relative biomass as a function of allocation algorithm and resource level.

However, the maximum biomass is only marginally improved with an increase of 6% for *fixed-equilibrium* and 8% for *fixed-optimisation* in low resource condition (see figure 2.4). These percentages drop to less than 1% in high resource availability conditions. The *plastic-optimisation* algorithm even leads to a decrease in the maximum biomass averaging 10% and 13% respectively in low and high resource availability conditions.

Figure 2.4: Maximum biomass relative to the *non plastic* simulations, as a function of allocation algorithm and resource level.



The effect of plasticity on the potential diversity is estimated by looking at the species that reach the range of 90% to 100% of the maximum biomass within the specific conditions (for each parameter set, algorithm and condition separately).

PHENOTYPIC CONVERGENCE

The number of species within this range is extremely low in *non plastic* allocation algorithm simulations, with 1.4% and 2.1% respectively for low and high resource conditions. This percentage is greatly improved by plastic allocation algorithm and reach in average 9% to 15% of species in *fixed-equilibrium* and *fixed-optimisation* algorithm, while it can reach up to 100 % for *plastic-optimisation* algorithm, with a mean proportion of species with a top performance around 72% in low availability condition, and up to 82% in high resource availability condition.

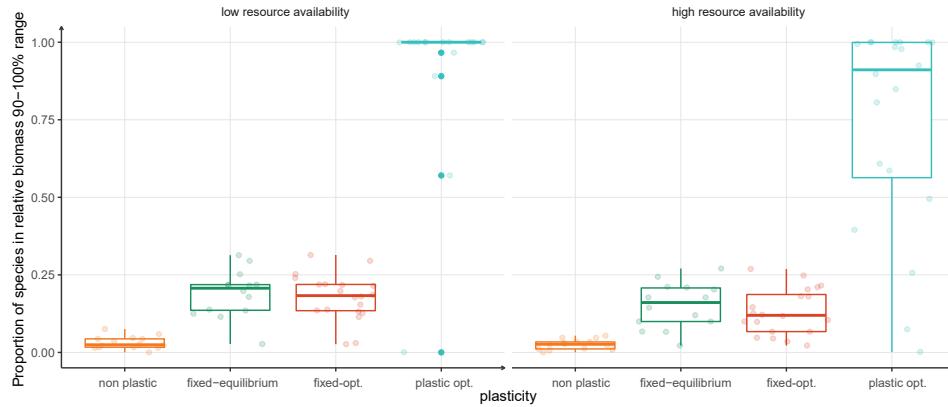


Figure 2.5: Proportion of species within the range of 90% to 100% of the maximum biomass, as a function of allocation algorithm and resource level.

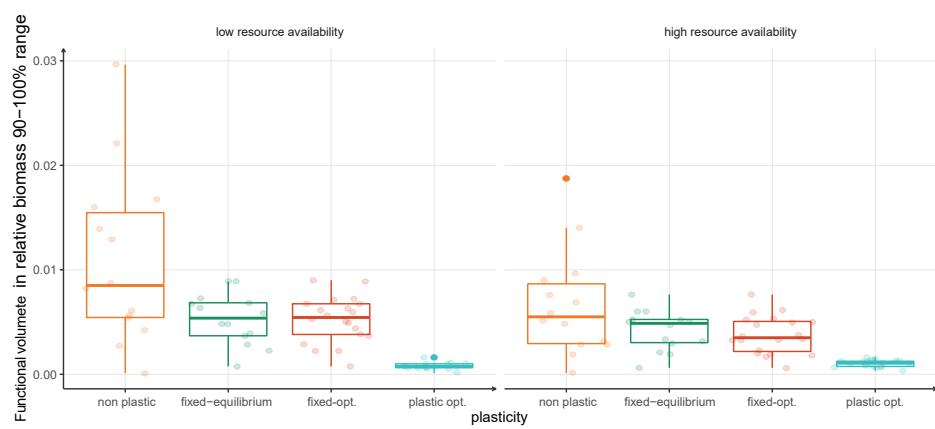


Figure 2.6: Functional volume occupied by the species within the range of 90% to 100% of the maximum biomass, as a function of allocation algorithm and resource level.

The functional diversity, estimated with the approximate volume of the top phenotypes, follows an opposite trend, with the highest value for the *non plastic* allocation algorithm. *Fixed* algorithms present half the functional volume of the *non plastic* algorithm, and the *plastic-optimisation* algorithm has extremely low values five times lower than the *non plastic* ones.

2.1.3 Discussion

The study of the performance landscape puts in light the different components of **plant performance**. To understand how plasticity can play a role, it is important to understand what makes a phenotype a good phenotype. On one hand, the extent of strategies (plan PAR-PAS in figure 2.1) with high relative growth (green area) is high when the best RMF is considered, while this is greatly reduced on plans that integrate RMF variability (see figure 2.7). This result suggests the high importance on this axis for the plants' performance. This can be explained by a stronger effect of this dimension on the exchange area through changes in organ masses, instead of organ densities (affected by PAR and PAS). The RMF fraction impacts the plant performance in two ways: by changing the **equilibrium** between shoot and root exchange activities, and by changing the global carbon loss rate (respiration and tissue turn-over) if the organs differ on this aspect. These two components may have opposed directions, as the limiting organ may also be the least efficient, and therefore the RMF could be greatly constrained if the two aspects have similar importance. The effect on the equilibrium is likely to be more important as a wide range of RMF values can be observed for numerous datasets (data not shown), and plant with uncoordinated (low-PAS & high-PAR, or high-PAS & low-PAR, see figure 2.7) organs still present high biomass values, suggesting that the respiration and turn-over loss are less important than a balanced resource acquisition.

COMPONENTS OF PERFORMANCE

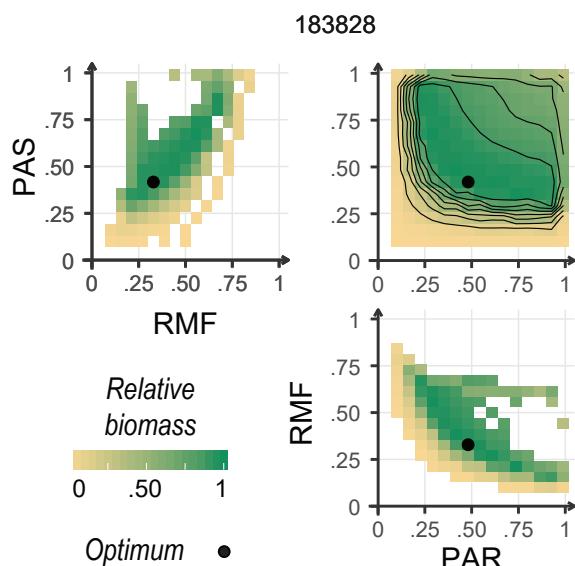


Figure 2.7: Projection for the parameter set 183828 of best phenotypes (according to the variable that is ignored) on 2D plans of the phenotypic space. The dots represent the optimum phenotype. White space indicates the absence of phenotypes able to survive until the end of the simulation (100 days). RMF: root mass fraction, PAR: proportion of active tissues in roots, PAS: proportion of active tissues in the shoot.

On the other hand, the organ-specific strategies are also important as low values for any of the organs (leaves or roots) lead to very low growth. Extreme high values can also be limiting, suggesting the existence of an optimum of the proportion of active tissue for the tissue efficient. This **optimum tissue efficiency** results from trade-off between active and structural tissues, driven by the

relative importance of carbon gain (increased exchange area with active tissues) and carbon loss (increased respiration and turn-over with the proportion of active tissues) that depends on models parameters and resource availability (that change the exchange rate).

However, meeting these tissues specific optima might not be sufficient, as the bean shape of the best phenotypes suggests, another component is relevant. Low values of the proportion of active tissue in one organ can be compensated by a high allocation of active tissues in the other organ that allows a higher allocation in the low exchange rate organ. This confirms the importance of the equilibrium over the tissue-specific strategies. But the shape also reveals a last component of the plant performances. The fact that species with high values of the proportion of active tissues in both organs have lower biomass, is certainly due to a limitation of both resources (equilibrium is assumed), reducing the overall efficiency.

From this visualisation of plant biomass as a function of the phenotypes, three main components play a role. The **equilibrium**, mostly driven by the changes in RMF is essential to the plant growth. This is explained by a reduction of the exchange rate of the non-limiting organ that greatly reduces its organ-specific efficiency. This **organ tissue efficiency**, driven by its effective exchange rate, respiration and turn-over, is also an important component of plant performance. Low values of allocation of active tissues greatly reduce this efficiency, but it can be compensated by bigger organs. However, such mechanisms can affect the overall efficiency defined as the average mean of organ realised efficiencies (taking into account resource limitations) weighted by the organ masses. Finally, the **speed** of the plant, or the overall resource acquisition rate, admits an optimum that is between an over-capacity leading to a co-limitation of resource on both organ reducing their individual efficiencies, and the under-capacity, leading to a sub-optimum use of resources and letting space for competition.

The phenotypic plasticity allows species to move within this performance landscape along certain axes. It is often perceived with a species-centric perspective, that is to say, that plasticity is seen as variations in the species mean phenotype. However, in the context of community ecology, it is also interesting to try to see how it not only affects individual species but shapes the community distribution in the strategy space. The plasticity relies on changes of default phenotypes toward "better" strategies in the context of the given conditions, therefore it implies that if it exists an optimum subspace (one strategy or an ensemble of strategies) species will converge toward this subspace, distorting the functional space. Environmental variations and plant interactions aside, in a constant environment the **performance landscape** is fixed. As a consequence, the plasticity benefits to the plant in a static manner, that is to say, it is only a tool to reach a better phenotype where the plant stays in if conditions do not change. This can be related to spatial heterogeneity that would lead individuals from the same species to adopt different phenotype to acclimate to the particular conditions of their spatial situation. It is opposed to the perception of a more dynamic phenotypic plasticity as a tool for a given individual to cope with temporal variations in environmental conditions. These two aspects are further discussed in the following section, while the effects of the contraction of the phenotypic space are discussed now.

As just mentioned, the plasticity can be seen at the scale of the species as-

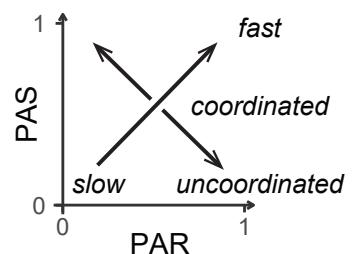


Figure 2.8: Alternative axes to describe the plant phenotypes on the plan PAR-PAS (PAR: proportion of active tissues in roots, PAS: proportion of active tissues in shoot). The slow-fast axis refers to the proportion of active tissues (close to the fast-slow strategies of Reich (2014)), while the orthogonal axis shows how coordinated the plant is (see Freschet, Swart, *et al.* (2015) for similar concept).

CONVERGENCE TO SUBSPACE

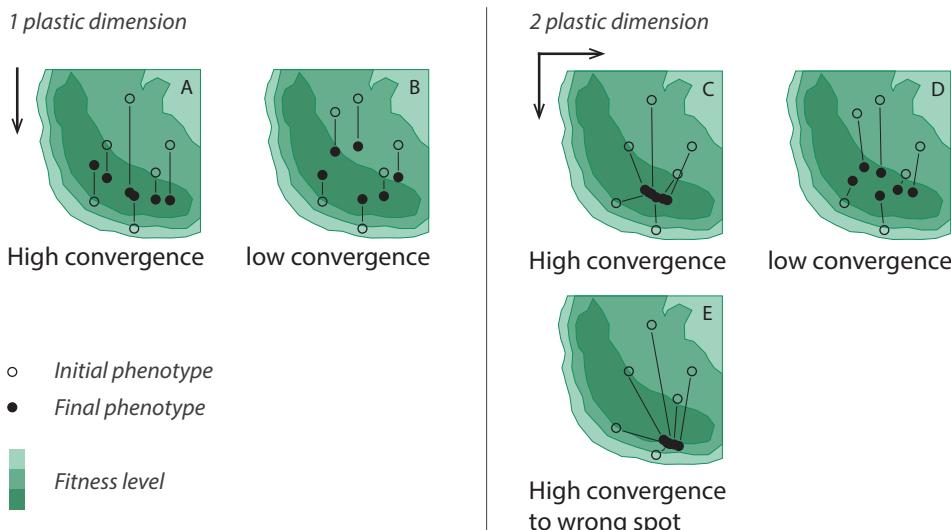


Figure 2.9: Convergence patterns on a 2D phenotypic fitness landscape, with 1 plastic dimension (A & B) or 2 plastic dimensions (C, D & E). Plasticity can lead to high convergence (A, C and E) with potentially high fitness evenness, especially in space with numerous plastic dimensions (A & E), this is problematic especially if the point of convergence is not the optimum (E). Limits to high convergence are necessary to allow realistic functional diversity with plasticity (B & D).

sembly¹ as a contraction of the phenotypic space of the species assembly. This contraction has two main effects: the reduction of potential functional diversity and a reduction of growth rate differences. There is here an emerging trade-off between the **species diversity**, supported by lower fitness differences, and **functional diversity**, reduced by the contraction of the phenotypic space. However, if the plasticity reduces greatly the potential functional diversity (volume of the whole phenotypic space without considering filtering based on relative fitness), the realised diversity (expressed as the functional diversity of the species within the 90%-100% maximum biomass range) is less impacted because a large parts of the phenotypic space have low growth rate in the given conditions. Nevertheless, there is a reduction in the diversity of expressed phenotypes. Indeed, in this scenario of "extreme" plasticity ($\tau = 0$) the convergence is important on plastic dimensions while partial convergence would be enough to have good fitness (see conceptual figure 2.9). Lower convergence on plastic dimension should lead to less compact phenotypic subspace while keeping relative fitness evenness. In the case of *fixed-equilibrium* and *fixed-optimisation* allocation mechanisms, this reduction of diversity is lower because only one axis is plastic.

A reduction of the phenotypic convergence can be achieved by other allocation mechanisms, differences in projection (different τ values leading to different projections) and plasticity costs. In a heterogeneous system, this convergence is expected to be lower as heterogeneity will lead to different projections. The constraints imposed by fixed traits also reduce the risk of convergence (lower convergence in panel A than in panel C in figure 2.9), and other dimensions than the 3 studied here can be involved in the definition of the optimum (chemical traits for example) lead to larger optimum sub-space.

The question of diversity is essential in ecology, it often refers to the species richness, or to different indexes to measure this richness or characterise the community structure. In the context of the ecosystem functioning and services, the functional diversity is often preferred to characterise the community. To measure the functional diversity, the selection of the measured traits has an importance. Once these axes defined, multiple indexes can be used, considering the relative species abundances or the distances between measured traits (Laliberté & Leg-

¹ Here I draw a distinction between species assembly that refers to all present species, and community that refers to the interacting individuals of the present species. However, some interpretations can be translated to communities.

ON DIVERSITY

endre, 2010). Here, in the context of simulations with species diverging only of the 3 vegetative phenotypic axes, the functional diversity is expressed an estimation of the functional volume occupied by the species with top performance within this 3D space. But, because under certain allocation algorithms, some dimensions are plastic, it is difficult to study how plasticity impacts the functional diversity. The plasticity of an axis can lead to convergence and certainly reduce the potential functional diversity as only a subspace is considered. This is problematic in this context because there is a high convergence due to the specific implementation of the plasticity based on a shared gain function (equilibrium or growth-optimisation), but is certainly reduced if the algorithm allow contrasted responses (with response curves for example), or optimum phenotypes depending on the other traits as it is the case for *fixed* algorithms (as opposed as the *plastic-optimisation* algorithm). Because of this phenomenon of convergence, that cannot be totally avoided and is inherent to the concept of plasticity, the functional diversity should be considered in relation with the species diversity. The functional volume is reduced by a factor between 1 and 2, while the species richness is increased by a factor from 5 to 10 (see figures 2.1.3, & 2.1.2). While the ratio between functional and species diversity decreases in plastic conditions, the overall effect on diversity could be positive, especially if there are other traits (non considered here) correlated to the initial phenotype.

The convergence of the phenotypes to a sub-space of lower performance lead to an increase in the mean biomass (see figure 2.4). However, the maximum biomass is only marginally improved in *fixed* plastic allocation simulations, and reduced in *plastic optimisation* allocation simulations. These two contrasting results show different effects of plasticity. The light increase can be due to either a dynamic gain or a static gain. The **dynamic gain** can emerge because the plant growth affects the resource availability, changing the optimum phenotype, and allowing plastic plants to follow these changes over time. It could also result from a **static gain** because the phenotypic plasticity allows a better resolution in tested phenotypes (the plastic axis are continuous while the phenotypic space sampling was discrete). The role of plasticity and dynamic gain is explored in the following sections with temporal resource heterogeneity.

LIMITED GAIN

The reduction of the maximum biomass highlights the difficulty to find the optimum phenotype. Because, the growth mechanisms are reproduced in an exact manner in the plasticity algorithm, this mismatch is certainly due to a difficulty to project the future of resource availability. Because of that, it is possible that the gain in maximum biomass, mentioned above, due to static or dynamic gain is greater than it appears. The particular case of mis-projection in *plastic-optimisation* simulations is discussed in the following paragraph.

Phenotypic plasticity can lead to a certain degree of convergence, especially if the target phenotypes defined by the implementation of the plasticity are more condition-specific than species-specific. While it can have strong effects on the functional diversity for the plastic traits, it also leads to high species richness due to a convergence toward a more performing subspace, and can potentially increase the total functional diversity if other traits are considered and the phenotypes more constrained.

The *plastic-optimisation* algorithm is characterised by a high convergence of the species within the phenotypic space, high mean biomass but maximum biomass

PLASTIC EXHAUSTION

lower than best *non plastic* phenotype, and high potential species diversity. The convergence is expected and explained by the fact that all three traits are plastic and all species (for a given resource level) experience similar conditions leading to the computation of the same optimum. The absence of plasticity cost limiting the convergence leads to a phenotype concentration toward this optimum. This convergence explains both the high potential species diversity, as all species have very similar growth rate, and the relatively high mean biomass because only a few species did not survive or had very little growth rate.

The fact that this plasticity does not translate into higher maximum biomass is surprising, especially considering the fact that RMF plasticity improves maximum biomass (see figure 2.3). Lag in adaptation is often identified as a limit of plasticity (DeWitt *et al.*, 1998; Van Kleunen & Fischer, 2005), nevertheless, in a constant resource influx experiment, and considering the high phenotypic flexibility of plants in *MountGrass*, this explanation is unlikely. Another problem highlighted with plasticity is its adaptiveness. Evolutionarily speaking, it is hard to imagine the emergence and maintenance of a plasticity mechanism (in a given context) if it is no adaptive. Yet, such process could be maladaptive in a new context. Because plasticity is not emerging but imposed by the simulation set up, its adaptiveness can be discussed. Here adaptiveness does not refer to a reduction of fitness due to plasticity but to the capacity of the plastic mechanism to define an optimum (or at least better) phenotype. Plasticity, as implemented in the model, has no explicit bias and all mechanisms involved in plant growth are simulated by the allocation algorithm. The sampling of phenotypes is random and could be a source of uncertainty, but it is uniform and no consistent drift is likely to emerge from the noise introduced by such sampling. The last aspect of plasticity that can affect the adaptiveness of plasticity is the estimation of conditions. The estimation of conditions is based on the resource levels experienced by the plant and by definition are exact. Thus, the problem lies in the projection of these conditions and how they translated into resource uptakes.

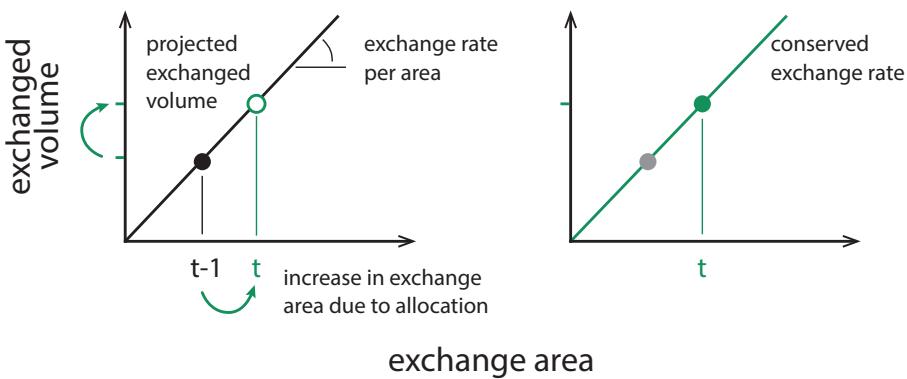


Figure 2.10: Projection of the water volume exchange after increase in exchange area at equilibrium and with no limitation.

In *MountGrass* the resource availability is coded as an uptake rate per day and per unit of exchange area and is computed as the resource uptake divided by the exchange area. This resource availability is supposed constant, and plants make the assumption that increasing their exchange area leads to a proportional increase in resource volume exchanged (see figure 2.10).

However, in the case where a plant already absorbs all the available resource, then this assumption is not respected, and the uptake rate per area is lower

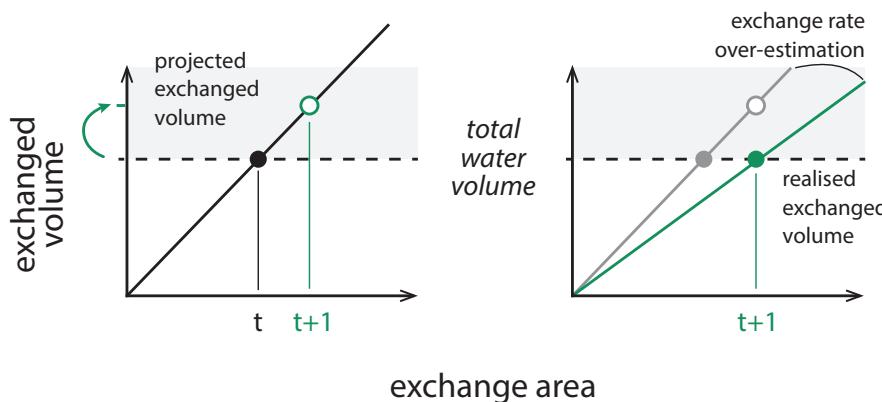


Figure 2.11: Projection of the water volume exchange after an increase in exchange area when total available water volume is limiting. The water volume exchanged cannot exceed the total available water volume, leading to a systematic over-estimation of water availability and offset between shoot and root activity.

than expected (see figure 2.11 right panel, realised exchanged volume does not match the projection because it cannot exceed the total volume of available water). This gap between perception and actual resource availability occurs because the plant is not able to perceive that the limitation cannot be compensated by a higher investment in the limiting organ. This behaviour explains a very high investment toward root and root active tissues in low resource conditions under *plastic-optimisation* allocation (figure 2.2). This gap¹ is the cause of the **plastic exhaustion** phenomenon. Indeed, this constant over-estimation leads to a constant discrepancy between the estimated optimum phenotype and the actual phenotype, and a larger allocation to root active tissues. This effect is particularly noticeable in the context of pot simulations where the water pool is limited. The absence of plasticity costs also favours such extreme behaviour.

Despite this particular, seemingly non-adaptive behaviour, the *plastic-optimisation* algorithm is still interesting to study in the context of community simulations. First, the presence of plasticity cost should limit such extreme behaviours. Second, in a context of competition in a larger environment, this aggressive search behaviour is likely to be an advantage against individuals with less aggressive, or stable strategy. Finally, this mechanism emerges in constant influx conditions that allow growth, but its emergence should be reduced in a variable environment where water shortage leads to reduced growth.

The plastic exhaustion mechanism seems to be contradictory with the previous observation that the proportion of active tissues does not increase when the related resource is limiting (see figure 1.12), but it can be argued that in such extreme case, if the RMF has extreme values and is constrained by differences in tissue efficiencies. This is not verified, however.

Plastic-optimisation simulations expose large amplitude of plastic exhaustion. This effect is possible with other allocation algorithms, but with negligible amplitude. The difference in magnitude can be explained by a less effective growth in early stages of development for *fixed* plasticities (when *plastic-optimisation* is more efficient than *fixed* plasticities) that delay the time when the total volume is reached (time t in figure 2.11), and in average lower active tissue allocation in roots that leads to lower loss due to non-equilibrium.

Plastic exhaustion is a specific limit of phenotypic plasticity as implemented in *MountGrass* that relies on the assumption of constant exchange rate per exchange area. It has a large effect in the specific case of pot simulations. This

¹ this is different from a lag because it is not the result of slow changes in phenotype but comes from a default in the estimation of the optimum phenotype.

mismatch between the projection and the reality of environmental conditions lead to an unbalanced phenotype and a large reduction in growth rate. However, this phenomenon can be mitigated by plasticity cost linked to changes in traits and can have adaptive value in a context of competition. Therefore, I argue that *plastic-optimisation* algorithm has low information value in the context of pot simulations with constant resource influx, but should still be studied in the context of community dynamics.

As expected the resource availability and the resource balance are key components of the plant growth, to which the plant phenotype needs to match. Aside from the increase in biomass, an increase in "speed" of optimum phenotypes can result from higher resource availability. This observation is in agreement with empirical data that demonstrate higher SLA and faster physiology in favourable conditions. This aspect was less obvious in the response of species under *plastic-optimisation* allocation that shifted more in term of balance and RMF. This may be due to a change in the relative balance between both resources as their availability (from the plant perspective) are linked to the global resource levels by non-linear relationships.

RESOURCE AVAILABILITY

The fact that plastic plants (for *fixed* allocation algorithms) show shifts of optimum strategies toward more exploitative phenotypes, in addition to the *non plastic* optimum shifts, in conditions of higher productivity demonstrate the importance of these strategies for the plant growth. However, the extent of this effect of conditions on optimum phenotype is susceptible to vary along a gradient. Indeed, because of the non-linearity of relationships between resource levels and exchanges rates, and between exchange rates and growth rates, the link between the optimum phenotype and a resource gradient is likely to be non-linear itself. In addition, phenotypic plasticity might also change the sensitivity of the phenotype to the resource level.

The study of the performance landscape highlights the importance of the RMF phenotypic dimension to regulate the balance between shoot and root. On the other hand, the proportion of active tissues in the two compartments impacts the performance in a more subtle way with the possibility of balance between the two organs thanks to the RMF. It also highlights the existence of a tight sub-space with higher performances, leading to high convergence under plastic allocation. This convergence can be problematic if the plasticity fails to be adaptive under specific circumstances. It can lead to a reduction of the functional diversity, but also increases the species diversity, altering the species-functional diversity relationship with potential consequences on the community functioning. The performance landscape is sensitive to the global resource availability, altering the relative fitness of species and their competitive relationships. This effect must be further studied to understand the link between the optimum phenotypes and the resource availability heterogeneity, and how plasticity can impact this link.

2.2 Plasticity and variability of conditions

The heterogeneity of conditions is an essential mechanism for plant coexistence. Plasticity is likely to alter the effect of this heterogeneity on plant coexistence and relative performance. The impact of plasticity on this relationship between spa-

tial and temporal **heterogeneity** of resources (here limited to water) and strategy dominance is explored with the model *MountGrass*.

How does plasticity impact the performance of the different phenotype along a resource gradient? How can these potential changes affect the identity, diversity and productivity of mountain grassland communities?

2.2.1 Method

Because the coordination is shown to be less important than the equilibrium, the below-ground resource acquisition is expected to be important in mountain grassland under climate change scenarios, and an extensive simulation plan comes with a high computational cost, only root strategies are sampled and studied in this part. Considering the structure of the model, the conclusions about the root compartment can certainly be extended to the shoot compartment.

For each of the 20 selected parameter sets, the growth of 400 plants (20 PAR values between 0.25 and 0.95, and 20 memory values between 0.1 and 1) is simulated for 100 days in square pots of 12 centimetres deep and 90 centimetres wide (to avoid quick self-competition) in a temperature of 20 degrees Celsius during the day of 15 hours, and 10 degrees during the night. The radiance is set to the high values of 122 Watt per hour and per square metre. Because *fixed* algorithms showed similar results, and the *plastic-optimisation* algorithm show strange results, only two allocation algorithms are simulated: *non plastic* and *fixed-equilibrium*.

SIMULATION SET-UP

Spatial heterogeneity of water level is mimicked by a gradient of water influx. The growth of all 400 species described above are simulated for *non plastic* and *fixed-equilibrium* algorithm independently in separated simulations where the water influx is regularly sampled between 0.05 and 7 mm per day (20 values).

SPATIAL HETEROGENEITY

A similar set-up is used for temporal heterogeneity simulations. Because the range of water influx used in the previous simulation is too wide, a lower value is chosen as the mean water influx. This value of 1.3mm per day corresponds to a point around which there are variations in the optimum strategies for most parameter sets. It is also relatively close to average rainfalls in the Alps during summer.

TEMPORAL HETEROGENEITY

2.2.2 Results: gradient of homogeneous precipitation conditions

To study the effect of plasticity on community identity along with a precipitation gradient, we can look at the position of the optimum strategy (PAR) along with such gradient with different allocation algorithms.

OPTIMUM STRATEGY

The effect of allocation algorithm is observed on all species by plotting the position of the median *optimum* along the watering gradient that translates what part of the strategy spectrum (from conservative to exploitative) benefit from the simulation conditions. At the low end of the gradient, conservative species exhibit higher growth than exploitative species with a median optimum around 25% of active tissues in roots for both the *non plastic* and the *fixed-equilibrium* plastic allocation. In the other end of the spectrum, for watering values above 1 mm per day, the *optimum* reaches a high point (median around 90% of active tissues for both algorithms) demonstrating the better performance of the exploitative

species in high resource availability conditions. There are no apparent differences between algorithms and the optimum is conserved along the gradient. There is a similar shift with an increase of optimum water availability memory for *non plastic* algorithm.

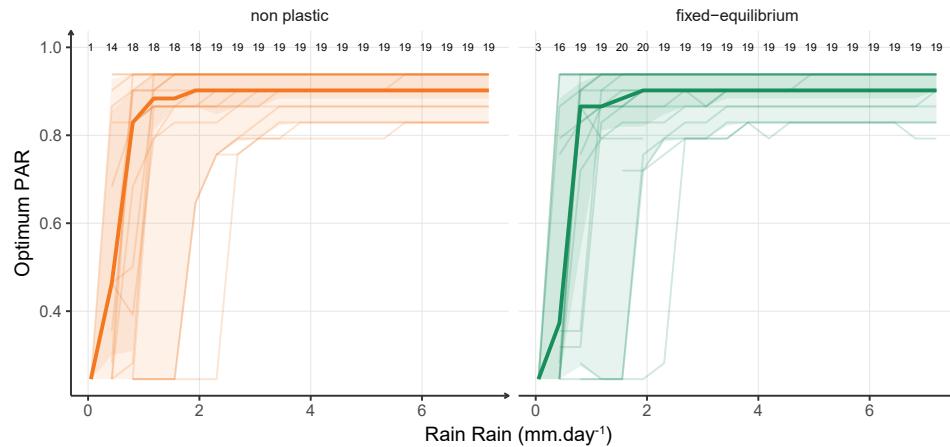


Figure 2.12: Median (bold line –) optimum root strategy along the water treatment gradient for – *non plastic* & – *fixed-equilibrium* allocation algorithms. The light lines (–) correspond to the 20 independent parameter sets. The color ribbon marks the band between the 5th and 95th percentiles.

The memory of water availability of best-performing phenotypes increases along the gradient under *non plastic* allocation (see figure 2.13, left panel), but the plasticity negates the effect of this species-specific parameter and no clear pattern can be observed (right panel).

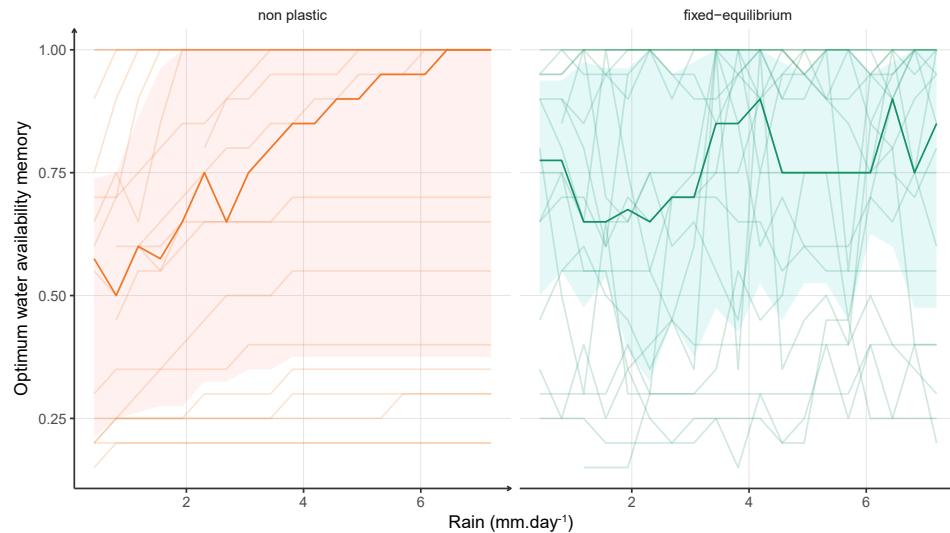


Figure 2.13: Median (bold line –) optimum water availability memory along the water treatment gradient for – *non plastic* & – *fixed-equilibrium* allocation algorithms. The light lines (–) correspond to the 20 independent parameter sets. The color ribbon marks the band between the 5th and 95th percentiles.

The total cumulative biomass of all plants increases along the precipitation gradients. The plastic simulations have a cumulative biomass that is twice the biomass of *non plastic* simulations.

PRODUCTIVITY

The effect on the maximum biomass is also investigated. For most simulation the maximum biomass is unchanged, and the median of the maximum biomass follow the same path for both conditions. However, the 75th and the 95th percentiles of plastic simulations show a high increase in maximum biomass.

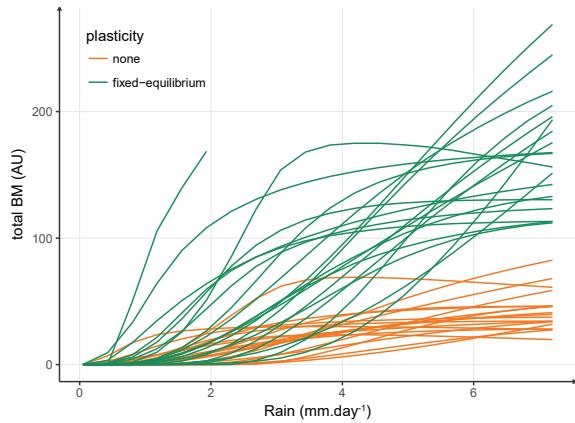


Figure 2.14: Total biomass of all individual along a precipitation gradient for all tested parameter sets. Colour distinguishes plasticity treatments: – *non plastic* & – *fixed-equilibrium*.

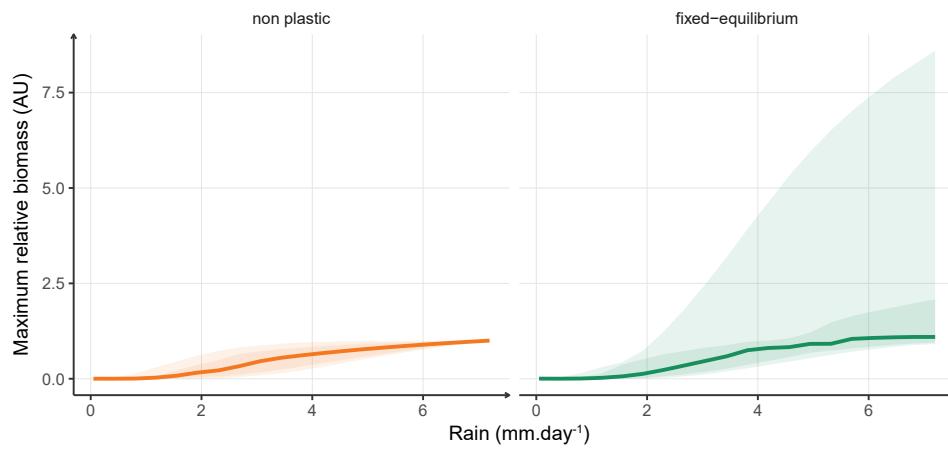


Figure 2.15: Median (bold line –) maximum biomass relative to the best performing plant in the most favourable condition for each parameter set, along a precipitation gradient. Colour distinguishes plasticity treatments: – *non plastic* & – *fixed-equilibrium*. The color ribbons mark the bands between the 5th and 95th and between the 25th and 75th percentiles.

Similarly to the previous results, the potential diversity is estimated with the number of species, or the functional volume, of the species within the 90%-100% range of the maximum biomass for the given conditions.

DIVERSITY

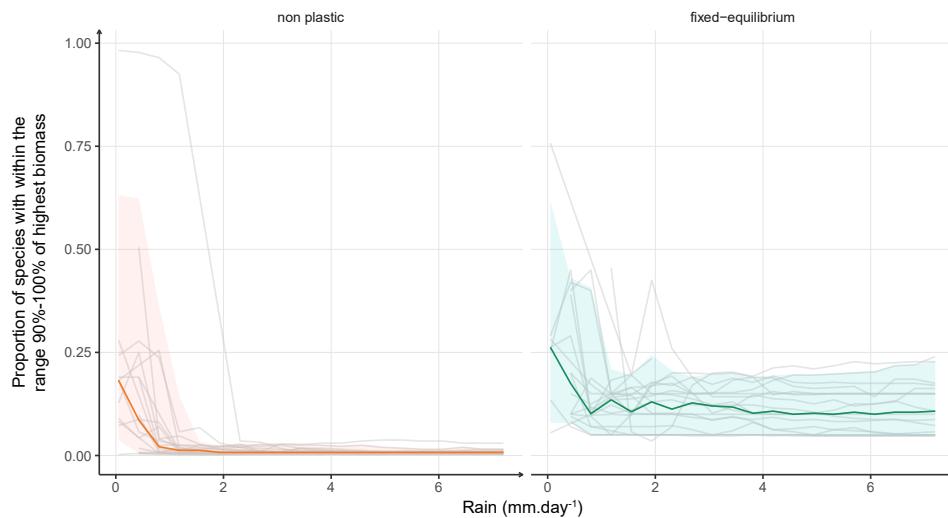
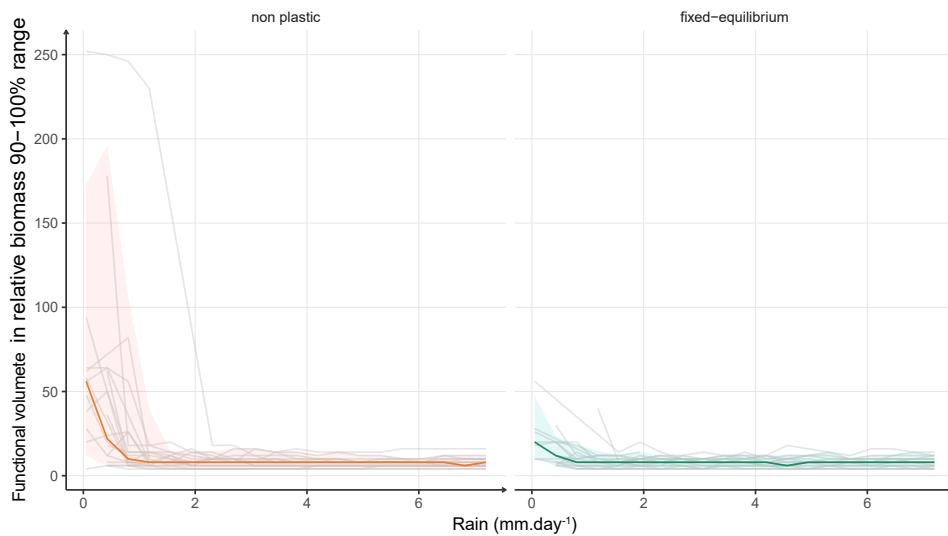


Figure 2.16: Median (bold line –) species richness of the species within the range 90%-100% of highest biomass for any given condition (parameter and precipitation) along a precipitation gradient. Colour distinguishes plasticity treatments: – *non plastic* & – *fixed-equilibrium*. The color ribbon marks the band between the 5th and 95th percentiles.

The species richness decreases along the gradient under the two plasticity treatments. The medians of species richness reach the low point for the same precipitation values than the medians of the optimum reach the highest values. The *fixed-equilibrium* simulations show highest species richness along the whole gradient (except for one parameter set).

Figure 2.17: Median (bold line –) estimation of the functional volume occupied by the species within the range 90%-100% of highest biomass for any given condition (parameter and precipitation) along a precipitation gradient. Colour distinguishes plasticity treatments: – *non plastic* & – *fixed-equilibrium*. The color ribbon marks the band between the 5th and 95th percentiles.



The functional volume occupied by the top species also decreases for both plasticity when the precipitations increase. For low watering values the functional volume of *non plastic* simulation is higher, however this difference disappears when both groups of simulations reach low functional diversity.

The median performance of the best performing phenotypes for each condition of the gradient is compared with and without RMF plasticity (*fixed-equilibrium*) along the gradient. It is limited to the best phenotypes to mimic a degree of

FUNDAMENTAL NICHE

biotic filtering. The plasticity greatly enhance the ability of the plants to maintain a high growth, often comparable to the one of the best phenotype, along the gradient. The extreme low value of the gradient shows no differences between phenotypes because the water level does not allow plant to grow, only the organic matter content is the seed is used, leading to similar outputs. As seen in figure 2.12, the best phenotypes often share the same strategy, but differ in memory for resource availability (figure 2.12). Under *fixed-equilibrium* allocation (right panel), the left end of the gradient (except the first value of precipitation) shows more contrast in the performances in strategies, while the right end (more water) shows very little contrast. This is very different from the *non plastic* allocation results (left panel) that shows large differences between the best strategies along the whole gradient.

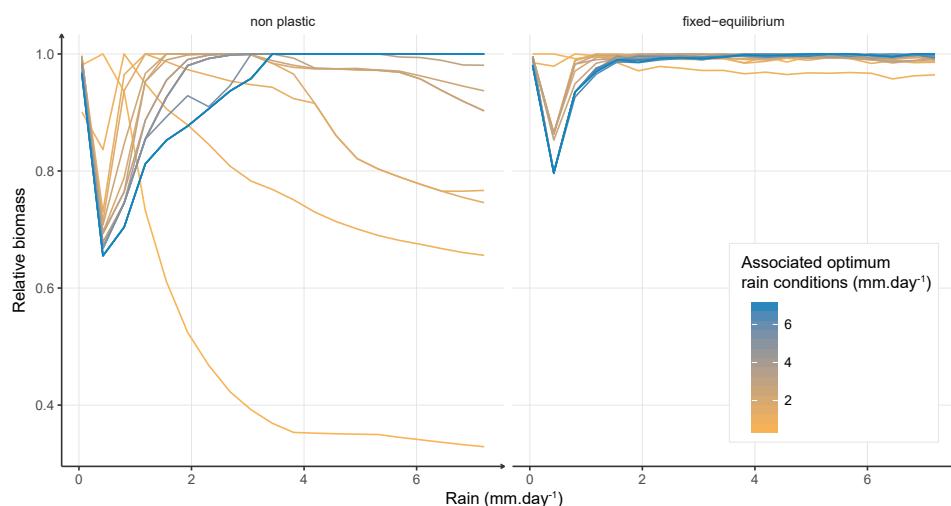


Figure 2.18: Median relative performance of best phenotypes along a precipitation gradient for 20 parameter sets.

2.2.3 Discussion: gradient of homogeneous conditions

Along the watering gradient, the **optimum strategy** (active tissue allocation in roots) changes from conservative toward exploitative. This shift demonstrates that the trade-off between active and structural tissues allocation allows different strategies to dominate in contrasting conditions (Wright *et al.*, 2004). This shift occurs for low values of the gradient and exploitative strategies are dominant over a large part of this gradient. The shape of the relationship results from the gradient including high precipitation values. Also, the low resolution of the strategies (15 values for the proportion of active tissues in roots) limits the possible number of different dominant strategies along such gradient. Because we can see a wide range of optimum of resource-use strategies, and the relationship between this variable and the resource availability is certainly continuous, we can be confident with the pattern observed and a positive relationship between these two variables.

STRATEGY SHIFT

The optimum memory also shows a shift, from low water availability memory in low water conditions, to high values in high water availability conditions. This response is less strong than for the optimum strategy certainly because the relationship is more linear. The fact that the plasticity negates this relationship confirms the role of this variable as a control on the RMF, control that is no

longer useful under plastic allocation with no cost.

This shift in memory is trivial to understand as the memory of light availability is fixed and the ratio between light and water memory controls the RMF. An increase in the memory (for *non plastic* plants) translates directly in a reduction of the RMF. The shift in optimum is less obvious, despite being described in the literature. The core of this trade-off is the trade-off between tissue efficiency and exchange rates. The more conservative species are more resource-efficient as they consume less resource to produce a bigger amount of organic matter, allowing them to be productive even in low resource conditions. On the other hand, exploitative species have a lower resource-efficiency but can exchange more resources thanks to high exchange rates per unit of biomass. This differences are illustrated in the figure 2.19, in high resource availability conditions (left panel) the exploitative species B show higher growth, despite having lower efficiency (costs relative to gain are higher), while its growth is lower when the gains are reduced linearly by a reduction of the exchange rate due to lower resource availability.

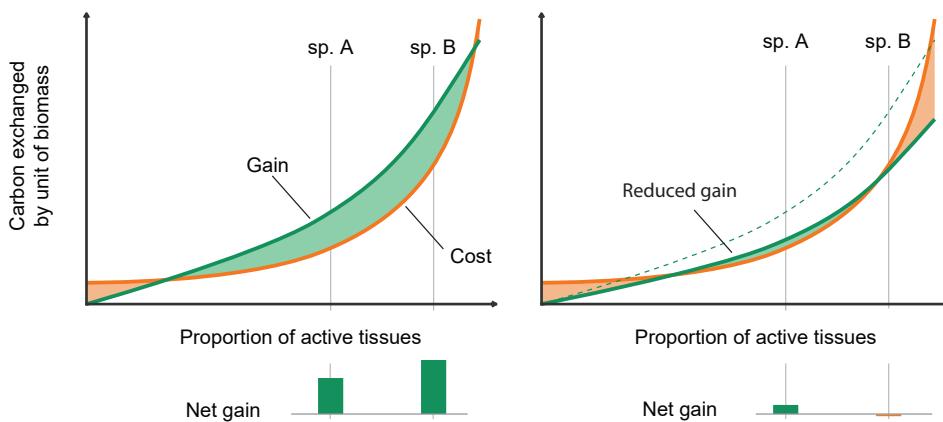


Figure 2.19: **Gain** and **losses** curves along the allocation strategy axis for one organ. Left panel corresponds to a high resource availability, the right panel illustrates the effect of a 30% loss of gain due to a reduction of the resource availability. The bottom bar plots represent the net gain of two distinct phenotype in the two conditions.

The maximum exchange rate influencing the slope of the gain function not only depends on the resource availability but also the non-limitation by the other organ or by regulation functions (see examples in Lohier (2016)).

When the limitation of the exchange rate is only dependent on the conditions, and the equilibrium is insured by the optimum RMF, in constant conditions the phenotypic plasticity cannot alter the optimum phenotype. This result supports the idea that plasticity should not induce a shift in the dominant strategy if the environmental conditions are stables.

The cumulative productivity of all species combined is largely improved by the plasticity for all parameter sets (see figure 2.2.2). However, the best total biomass is only improved for a fraction of these parameter sets (see figure 2.15), while it remains similar in most of others parameter sets between *non plastic* and *fixed-equilibrium* simulations. This observation supports the idea that the total biomass is mostly increased due to an improvement of plants with a non-optimum phenotype, and not an improvement of the best phenotypes. Moreover, while the number of species reaching high-performance levels increases with plasticity (corroborating the previous conclusion), the functional diversity does not increase. We can conclude that the phenotypic plasticity leads to a convergence of the plants toward good performance phenotypes. Therefore, the productivity

STATIC GAIN

gain provided by the plasticity comes mainly from the convergence toward the best fixed phenotype, and cumulative static gain.

This form of gain provided by the phenotypic plasticity can be called **static gain**, as it is capped by the best performing constant phenotype. It is illustrated in the figure 2.20. The gain only comes from the transition from a sub-optimum phenotype toward the best one (see **starting phenotype A** shifting toward the green one). The gain can be quantified as the total biomass difference between the non plastic species (- - dashed line) and the plastic one (- continuous line). In constant condition, the best phenotype cannot benefit from the plasticity because it has the highest growth rate along time and has no static gain (**starting phenotype B**).

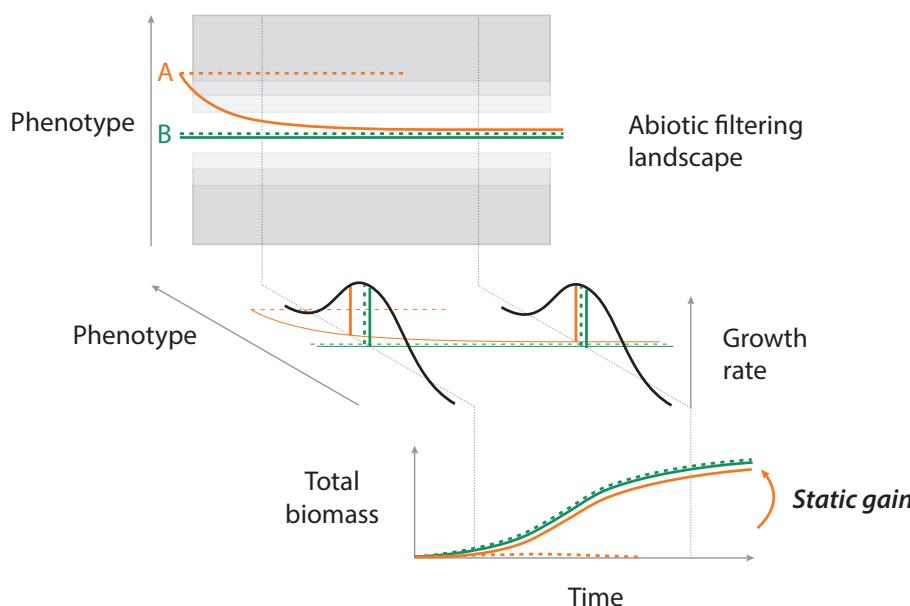


Figure 2.20: Conceptual representation of the abiotic filtering in constant conditions and the illustration of the static gain. The top panel represents the abiotic filtering landscape with a central valley and the trajectories of the species. The middle panel is the growth rate as a function of the phenotype for two positions in time. The bottom panel illustrates the growth curves for the different phenotypes. Two alternative position **A** and **B** represent a sub-optimum and the optimum position without plasticity (dashed lines). Alternative plastic trajectories are represented by continuous lines.

The static gain allows species to persist in environmental conditions that do not fit their initial phenotype (**A** – continuous line), and go through the **abiotic filter** while the non plastic equivalents (**A** - - dashed line) cannot. This reduction of the impact of the abiotic filter can have large impacts on the community properties.

The phenotypic plasticity of the RMF leads to an important widening of the fundamental niche. This is explained by the removal of one constraint of the niche. Indeed, with cost-free plasticity in RMF, the equilibrium is almost guaranteed for all species and the resource-use strategy is the only limitation of a species niche. Because the best proportion of active tissues is the same for a long portion of the gradient (high water availability)(see figure 2.12), along with the gradient most of best phenotypes share this resource-use strategy. Therefore, along with this same gradient, if the RMF axis is ignored, the different species have equivalent phenotypes (except for a few first growing days).

This niche widening has for consequence a higher niche overlapping. This overlapping can be translated into lower niche differences, as the niches are now discriminated only on one dimension, and into lower fitness differences as the species with similar strategies but different memories have close performances under plastic allocation. According to Turcotte & Levine (2016) these two pro-

NICHE WIDENING

cesses have opposed effects (see figure 3.7 in chapter II) on the species diversity. On one hand, the reduction of the niche differences diminishes the positive effect of the spatial heterogeneity on diversity. On the other hand, the reduction of fitness differences reduces the competitive exclusion of the non-dominant species and limits the abiotic filtering. The current simulations do not allow to tell which effect will be the strongest at the community scale. The cost of plasticity should nevertheless ensure some degree of niche differentiation. In addition to these two effects, the widening of the fundamental niche corresponds to a reduction of the abiotic filtering pressure and should promote the diversity as more species can potentially invade a habitat.

The reduction of the abiotic filtering implies a potential increase in the biotic filtering due to the limited carrying capacity of the habitat. This could raise the competition intensity, especially at the beginning of the growing season, and eventually change the dominant species if this increase is strong enough to alter the competition outcome toward more competitive species. Unless the eventual new dominant species has a dramatic effect of the overall productivity or diversity, the effect of the phenotypic plasticity through the competition should be positive or null on these properties. But because the phenotypic plasticity does not alter directly the optimum phenotype in temporally fixed conditions, the impact on the dominant resource-use strategy should be rather limited.

COMPETITION EFFECT

While the effects at the community level are still hard to define, the phenotypic plasticity can alter the dynamic at the meta-community scale. Phenotypic plasticity, by reducing the abiotic filtering effect, allows for a stronger link between the communities as the chance to transfer from one community to another are higher. Therefore this mechanism has a positive effect on the stability of the ecosystem as species from unperturbed communities can invade, and partly sustain the properties and services of the perturbed community.

META-COMMUNITY DYNAMICS

In a context of global change, to survive two options are possible: (1) migrate to new habitat with suited conditions, (2) adapt to new condition in the same habitat. In this context, the phenotypic plasticity facilitates both the adaptation to new conditions in the same spatial habitat and the adaptation to a new habitat that match the ideal conditions only to a certain degree. By facilitating the adaptation to new conditions or habitat, the phenotypic plasticity reduces the relative importance of climatic variables compared to the competition as already suggested by empirical results (Alexander *et al.*, 2015).

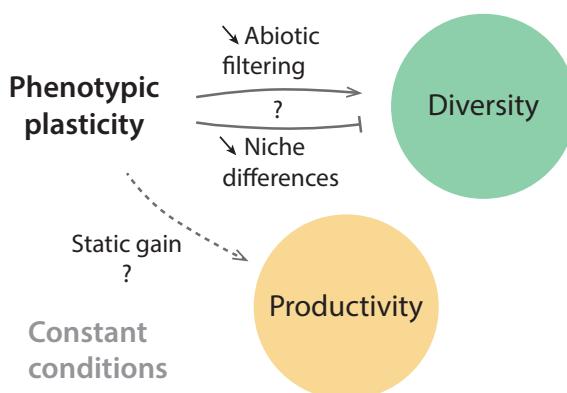


Figure 2.21: Effect of the phenotypic plasticity on the main properties of the grassland communities in constant conditions.

In constant environmental conditions, the phenotypic plasticity already has

an impact on species performances and interactions through the static gain it provides to some species. The species that benefit from this static gain have the optimum resource-use strategy, but a wrong estimation (memory) of the resource availability. It increases the fitness evenness of species by reducing the abiotic filtering dimensionality down to the resource-use strategy, axis not influenced by the plasticity. This leads to a convergence of the phenotypes and a widening of the fundamental niche. The effects at the community level are hard to anticipate, but they will be largely dependent on the competitive interactions and how they are affected by the plasticity. The reduction of the abiotic filtering will likely increase the species diversity, but the functional diversity might not follow this trend due to functional convergence. The effects on the other component of the ecosystem properties cannot be fully determined and greatly depend on the outcome of the competitive interactions. In temporally heterogeneous conditions, the phenotypic plasticity may play a larger role and greatly mediate the community's properties.

2.2.4 Results: gradient of heterogeneous precipitation conditions

This part of the chapter presents the results at the individual scale along a gradient of a temporal increasing variability of the underground resource (increasing negative slope of water influx).

The maximum biomass (relative to the *non plastic* best performance in constant watering conditions) decreases along the gradient for all allocation algorithms (see figure 2.22). The *non plastic* algorithm shows a drastic drop after the fourth level of variation, while the fixed-trait algorithms show better performances in this part of the gradient. The *plastic-optimisation* algorithm shows low growth for all conditions, but a more stable performance.

In contrast with the stable conditions (see previous results) the plasticity provide, in non-constant conditions a great improvement in the maximum biomass for most parameter sets.

In addition to a reduction of biomass, the increasing slope of the water influx reduction leads to a shift of the optimum strategy in *non plastic* simulations (see figures 2.23 & 2.24) toward more conservative strategies. The median optimum value shifts from 0.85 to 0.75 and 0.35 in extreme conditions. This reduction of optimum toward more conservative strategies is offset in most of *fixed-equilibrium* and *fixed-optimisation* simulations where the median optimum value for the PAR stays above 80%. Only a small reduction (around 25%) of the 5th and 25th percentiles of the optimum root strategy can be observed between the extreme conditions for these two algorithms.

This shift in optimum strategy can better be observed on the plan of the proportion of active tissues in roots (PAR) and root mass fraction (RMF) in figure 2.24 where all trajectories¹ along the variability gradient are plotted. *Non plastic* allocation trajectories by a linear shift toward more conservative strategies with a higher allocation to roots, while *fixed-equilibrium* and *fixed-optimisation* trajectories are non-linear and can be divided into two phases: (1) increase in RMF, (2) reduction of PAR. *Plastic-optimisation* algorithm shows no consistent pattern in trajectories.

PRODUCTIVITY

IDENTITY

¹ trajectory of the optimum, not of the species.

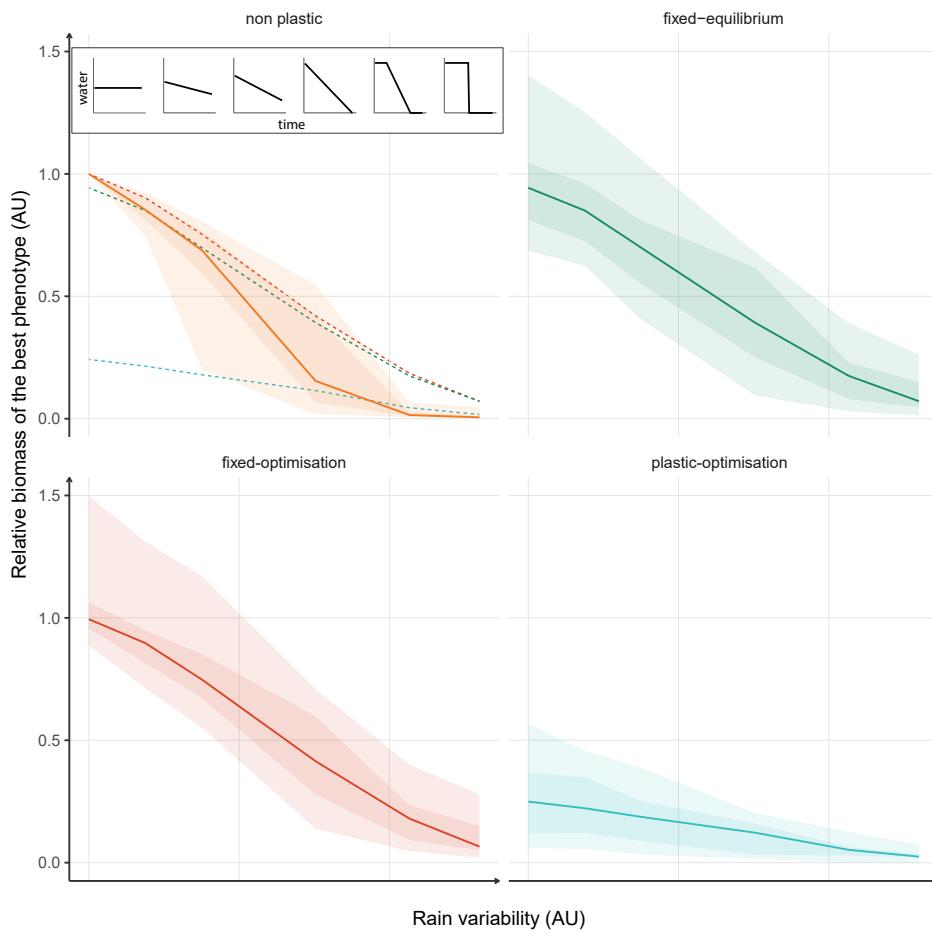


Figure 2.22: Median (bold line) biomass variation of the best performing species along a gradient of resource variability for four plasticity treatment. The upper panel of the top-left frame illustrates the water influx as a function of time along the variability gradient. The dotted lines in the top-left frame indicate the median biomass for the other three algorithms. The color ribbons mark the bands between the 5th and 95th and between the 25th and 75th percentiles.

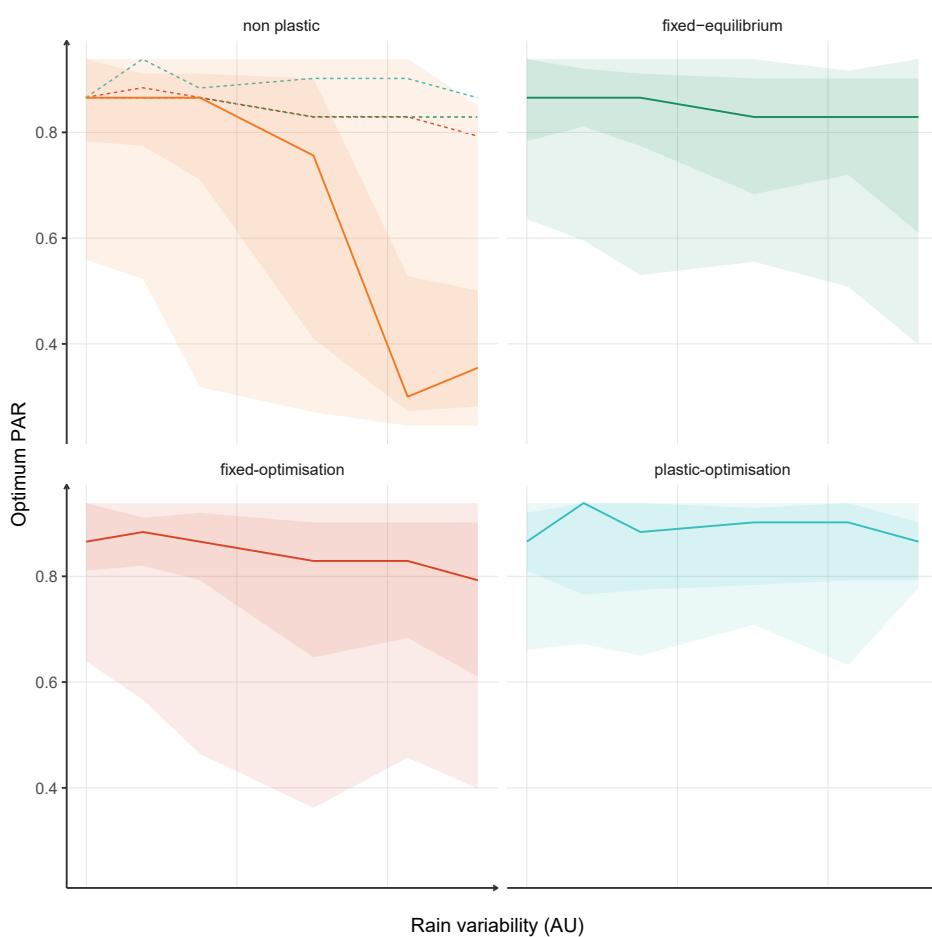


Figure 2.23: Median (bold line) strategy (PAR: proportion of active tissues in root) shift of the best performing species along a gradient of resource variability for four plasticity treatment. The dotted lines in the top-left frame indicate the median PAR for the other three algorithms. The color ribbons mark the bands between the 5th and 95th and between the 25th and 75th percentiles.

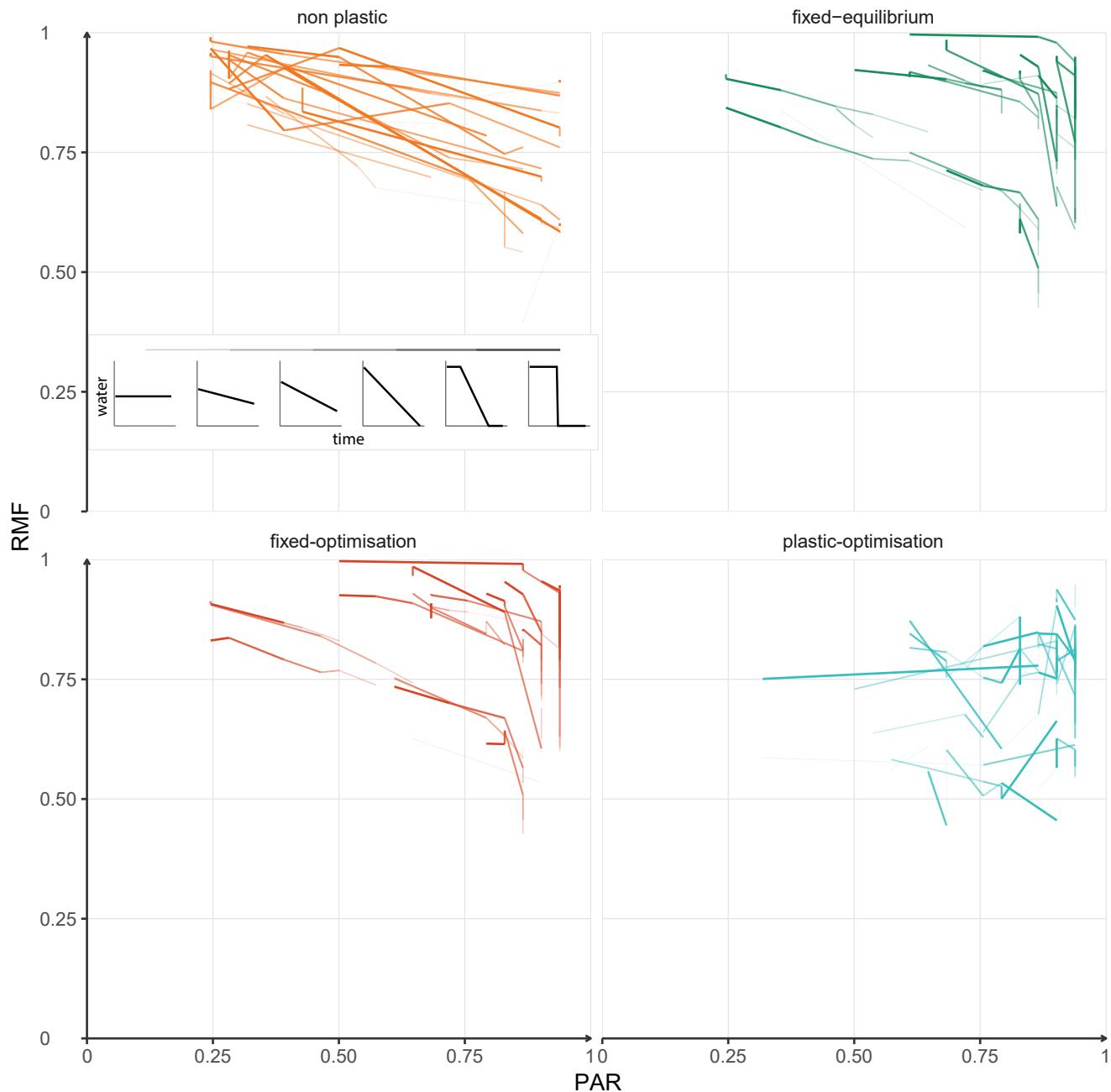


Figure 2.24: Best phenotypes along water resource variability gradient. Thinner lighter lines indicate low water variability, while the thicker lines indicate strong temporal heterogeneity.

DIVERSITY

Along the gradient, the performance and the identity of the bet phenotype were greatly altered by the water variability, but the phenotypic plasticity mitigates these effects. The number of species is fairly stable for all algorithms but the *non plastic* that shows an improvement in species diversity. The fixed allocation algorithms have between 15% and 20% of the species within the 90%-100% range of the maximum biomass for the conditions, while the *non plastic* allocation shows this level only of the extreme variable case, but otherwise is limited to a few percents. The functional diversity is stable along the gradient and is similar for all algorithms (*plastic-optimisation* algorithm being excluded)(data not shown).

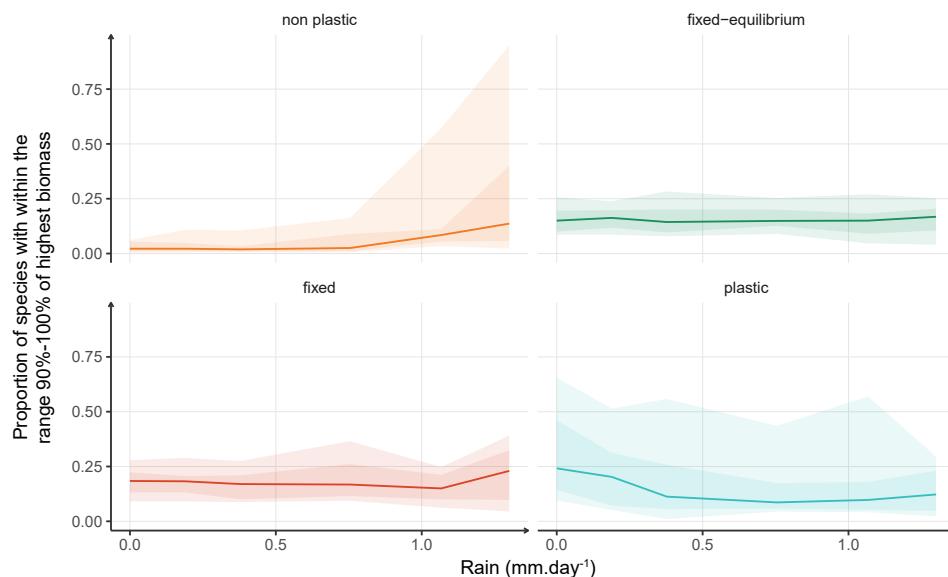


Figure 2.25: Species richness of the species within the range 90%-100% of highest biomass for any given condition (parameter and precipitation) along a water resource variability gradient. Colour distinguishes plasticity treatments: - *non plastic* & - *fixed-equilibrium*.

2.2.5 Discussion: gradient of temporal variations

Before analysing the effect of the different plastic algorithm, the *non plastic* simulations show interesting patterns. A first look at the results informs us of the relative importance of growing versus surviving. Because the mean water influx over the simulated period is conserved, an increase in the influx negative slope means that during the first half the plants have more available water, while they have less during the second half (relative to the constant influx). Thus, the decreasing biomass along the gradient suggests that this additional water (and therefore potential growth) does not compensate for a reduction in growth during the drought period. Therefore, it is more important for the plant fitness to limit losses during scarce period instead of maximizing growth during favourable periods.

However, this conclusion should be mitigated by the fact that some reproduction strategy still can benefit from early exploitative strategies and there are not considered here because the success is measured by the biomass after 100 days. This effect can be explained by the fact that even the most exploitative species are not fully developed when the resources are the most available, therefore the potential compensation by an early growth is limited. This is the case in the context of mountain grasslands, and some specific life cycle strategies take advantage of this particularity like the *galanthus* species (see figure 2.26) with early

RESISTANCE TO VARIABILITY



Figure 2.26: *Galanthus nivalis* is an example of species that develop early in the season to avoid competition and benefit from the high resource availability.

development (Schröder *et al.*, 2014), or development from a bulb that allows for an early and rapid growth.

The reduction of biomass along the gradient, even in plastic conditions, supports the idea of a lack of compensation mechanisms between favourable and unfavourable drought periods. In addition to this conclusion, the better performances of the conservative species in low water conditions relative to exploitative species (see figure 2.12) suggests that the best strategy is determined by the optimum resource-use strategy of the most important growth period (the drought period). However, another mechanism can be involved and is relative to the capacity of the species to perform well both in conditions that suit its phenotypes and in conditions that do not suit its phenotype. In a variable environment, the phenotype does not match conditions different from its niche centre because of the optimum resource-use strategy may change, or because of the balance between root and shoot activity changes. Both can be important. As said, the former is suggested by previous results, however, under plastic allocation, the optimum resource-use strategy is maintained at high values of the proportion of active tissues. Therefore, the difference in optimum resource-use strategy along the gradient cannot explain alone why conservative strategy is better in contrasted environments. The other explaining mechanism is a better resistance to variability from conservative species, relative to exploitative. The variability in water conditions, while the light conditions are fairly constant, leads to a shift in the balance in the availability of the two resources. If the phenotype is fixed, a shift from balanced conditions (equilibrium between shoot and root is respected for the given phenotype in these conditions) to unbalanced conditions (no more equilibrium for the same given phenotype) can be seen from the plant perspective leading to a reduction of the overall gain function stronger than the actual decrease in resource, because the non limiting organ is in over-capacity. Because they have a higher resource-use efficiency (see figure 2.19), conservative species can cope with this reduction in gain due to unbalanced organ activities. Therefore, in variable conditions, the optimum strategy shifts toward conservative strategies that have the capacity to support greater exchange rate reductions and have a greater **resistance to variability**. Under plastic allocation, the equilibrium is maintained, reducing the need for a strategy resistant to resource fluctuations. This is illustrated by the figure 2.24 that shows along the variability gradient a direct shift toward more conservative root strategies and greater root allocation, while under plastic allocation the shift toward conservative strategies is delay for stronger availability gradient, but the RMF shows larger values (they are measured at the end of the simulation, when the water availability is reduced).

The plasticity of the RMF axis allows plants to cope with resource availability and maintain exploitative strategies. These strategies are more sensitive to changes in resource levels under *non plastic* allocation than the conservative species that benefit from a greater resource-use efficiency.

While the phenotypic plasticity does not provide any clear advantage to a type of species in constant conditions, in changing conditions the phenotypic plasticity benefit to the exploitative species that are able to maintain good performances in contrasted conditions (see figure 2.23). Because the plasticity gain is asymmetric, the phenotypic plasticity alters the identity of the community and promotes exploitative species in variable conditions while conservative species are favoured under *non plastic* allocation. In a more theoretical view, the plasticity can be

WHO BENEFITS FROM THE PLASTICITY?

seen as an alteration of the strength of the stress as shaping factor of community (Grime, 1977). If the plasticity allows the exploitative species to better support stress, in modelling studies that do not take into account such plasticity, the amplitude of the stress needed to see a shift in the community identity may be under-estimated.

This **asymmetric gain** should favour already established species as it lowers the perturbation effect of climatic fluctuations. This stability is interesting for the maintenance of the ecosystem properties and services provided by the mountain communities. It also supports the idea of a greater resistance to climatic events that are expected to be more frequent under the climate change.

The plasticity has also an effect on the maximum biomass as observed in the figure 2.22. This effect is almost null in constant condition, as expected from the previous simulations, but increases with the resource variability. There is no evidence of improvement for all resource-use strategy, but because the unbalance caused by the temporal variability in resource greatly reduces the productivity, we can assume improvement of the biomass for all strategies. Therefore, the productivity between non plastic and plastic community under variable conditions should increase.

DYNAMIC GAIN AND STABILITY

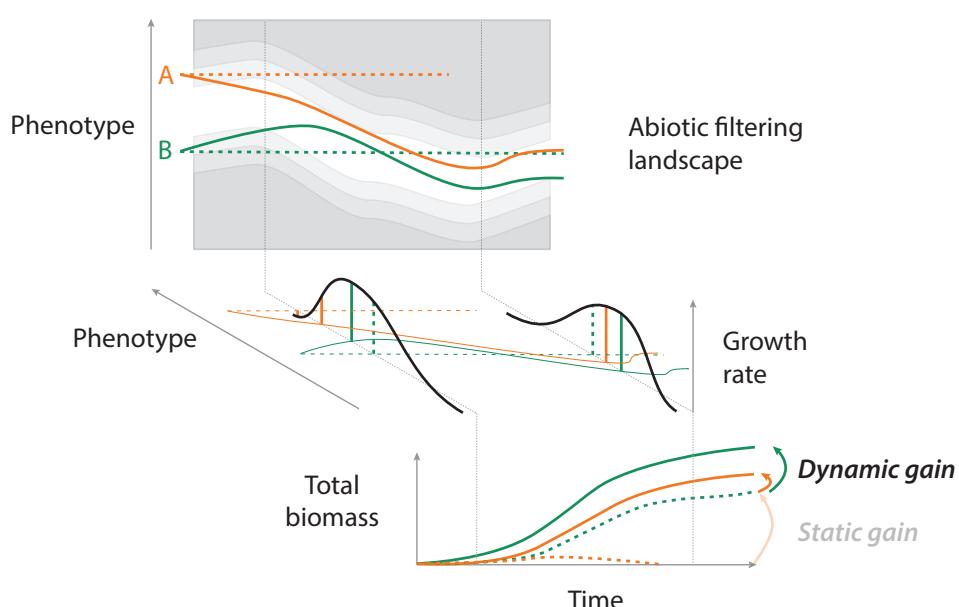


Figure 2.27: Conceptual representation of the abiotic filtering in variable conditions and the illustration of the dynamic gain. The top panel represents the abiotic filtering landscape with a sinuous valley and the trajectories of the species. The middle panel is the growth rate as a function of the phenotype for two positions in time. The bottom panel illustrates the growth curves for the different phenotypes. Two alternative position A and B represent a sub-optimum and the optimum position without plasticity (dashed lines). Alternative plastic trajectories are represented by continuous lines.

This is explained by the trajectories within the fitness landscape that can follow the changes in the optimum phenotype, and so present a total biomass superior to the best *non plastic phenotype* (see figure 2.27). The difference of biomass between a *non plastic* phenotype and its plastic counter-part (*fixed-equilibrium* or *fixed-optimisation*) is called the **dynamic gain**. This gain is not capped by the best *non plastic* performance.

The overall increase in productivity, in addition to the reduction of the abiotic filtering effect, should greatly increase the competition

The dynamic gain observed in temporally variable conditions has a similar effect on the abiotic filtering process than the static gain as the species are able to converge toward a moving phenotype and maintain positive growth, despite not having the best starting phenotype (see figure 2.25). However, in this context,

ABOUT DIVERSITY

this effect is even more important as it can allow species to establish in local conditions that not *non plastic* species could invade. In other words, it makes some habitats viable that would not be if there was not any plasticity. This effect can only be positive of species diversity because it is a net gain with no direct effect on competition.

While the trade-off between the functional diversity and the species richness is maintained, the asymmetric gain of plasticity may allow, if the costs of plasticity are considered, levelled fitness between conservative non plastic species, and plastic exploitative species.

The phenotypic plasticity in variable conditions shows similar processes that in fixed conditions. The convergence of the species toward an optimum sub-space leads to a reduction of the functional diversity but an increase of the species diversity. This reduction of the abiotic filtering should also increase the importance of the competition as a regulating process. However, it differs by an asymmetric gain that favours exploitative species, more vulnerable to changes in resource availability under *non plastic* allocation. In addition to this alteration of the community identity under plastic allocation, the productivity/competition intensity at a community level would be increased by a dynamic gain that improves the performance of the best phenotypes where the static gain does not (in stable conditions).

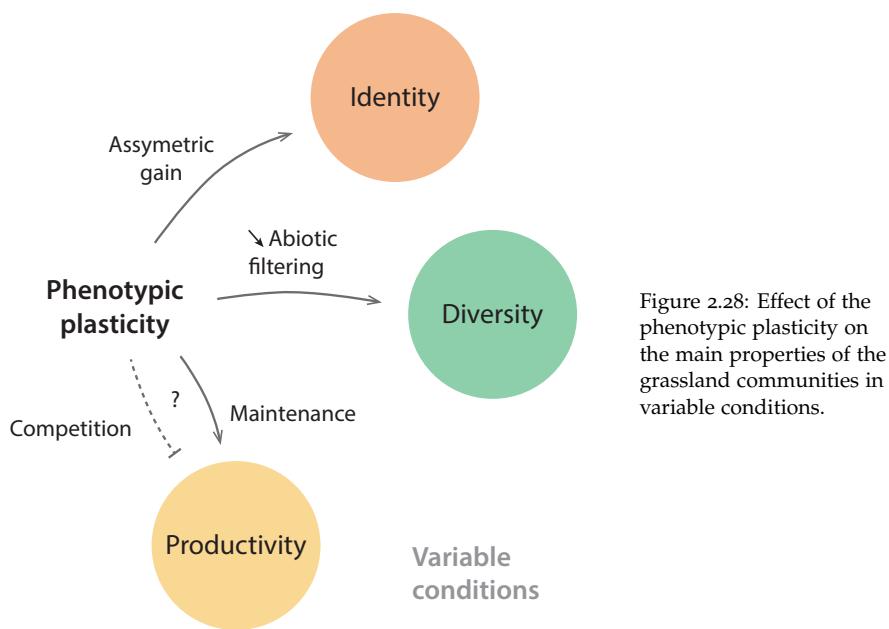


Figure 2.28: Effect of the phenotypic plasticity on the main properties of the grassland communities in variable conditions.

The phenotypic plasticity implemented in *MountGrassimproves* the relative performance of multiple strategies by concentrating the plant toward a subspace of higher performance for most of the plants. Convergence to a smaller subspace can be assimilated to a reduction in phenotypic diversity, but it reduces performance heterogeneity and should favour local plant diversity. However, this effect should be limited by plasticity cost. Indeed, if the growth gain due to plasticity is only static, any species with a fixed phenotype closer to the optimum than the focus species has a better growth rate and exclude the focus species. Community-level simulations are needed to further understand the cumulative role of competition, spatial and temporal variabil-

ity and plasticity costs on phenotypic plasticity influence on plant community dynamics.

2.3 Other plasticity patterns, alternative implementations and stability of results

The phenotypic plasticity implemented in the model *MountGrass* is the only way of modelling plant plastic responses, inspired by the tested hypothesis of the functional equilibrium, adapted to the light and water resources. Other patterns of plastic responses can be observed, and numerous alternative implementations can be imagined to reproduce these patterns. This section puts in parallel such plastic response pattern with alternative ways of modelling the phenotypic plasticity, and conjecture on the robustness of the results described above in these new modelling approaches.

2.3.1 Resource foraging and architecture plasticity

Phenotypic plasticity in the context of plant ecology is often related to resources gathering and use-strategies. While other forms of stress can be integrated, such as the grazing or frost events, the immobile aspect of the plant life and the inherent variability of resources encourage to focus on the resources needed to the production and maintenance of organic matter. The model *MountGrass* present a simplistic form to answer the changes in resource availability, relying on the hypothesis that the exchange rate is homogeneous and can be integrated at the individual scale. In case of heterogeneous resources, other modelling strategies may have better results.

In habitats where the abiotic stresses are low but the competition limiting, the resource foraging is a crucial mechanism to model. For example, in the context of forests, the observation of closed canopy reveals a relatively high crown plasticity leading to the incorporation of this phenomenon with techniques such as the tessellation (Berger *et al.*, 2008). Such technique has a limited cost, and suits well tree canopies with constant resource-use strategies, especially when only one resource is spatially-modelled explicitly, as it is often the case in forest models.

RESOURCE FORAGING

Nonetheless, such architectural plasticity is also observed within herbaceous species. In case of limiting light resource, the plants may adopt an etiolation strategy that aims to explore the 3D-space to find light (Whippo, 2006). This is an extreme case of morphological plasticity when the plant is bereaved of light, that leads to extreme changes in the shoot morphology - increases of the stem and leaf lengths, decreases of the leaf area - but also in the shoot chemistry - decrease in the tissue density, reduction of the chlorophyll content. Such response of increased SLA, reduction of the RMF and of the reduction of the chlorophyll content can be observed in less extreme cases of light reduction (Mitchell & Bakker, 2014). But the noticeable aspect of the plastic response to the reduction in light availability is the strong photo-tropism of leaves (Whippo, 2006), strongly altering the architecture of the plants.

Such architectural plasticity is also observed for roots, sensitive to nutrients and water levels. Multiple aspects of root architecture can be modelled as plas-

tic, while the root depth is often used, the vertical root distribution can also vary (Nippert & Holdo, 2015) as well as the horizontal distribution (Maire *et al.*, 2013), with beneficial impacts on the individual and community efficiency and productivity.

Despite a form of plasticity that answers changes in resource availability, the current implementation of *MountGrassis* is not able to reproduce such patterns. Indeed, these foraging behaviours are incompatible with *MountGrasson* two major aspects. First, the morphology and chemistry axes are independent (Mitchell & Bakker, 2014) while the design of *MountGrassries* to encapsulate multiple dimensions along the LES with simple allocation trade-offs. The drastic contrast in function between functional enlighten leaves that balance light capture and gas exchanges to maximise the production of organic matter, and the etiolation leaves that explore the 3D-space at low cost to find resource cannot be captured by the simple representation of the shoot, neither the objective functions that drive the plastic allocation. Second, such exploration of the space requires a spatial awareness and an architectural plasticity that cannot work with a cylinder representation of individuals. Voxel-based approaches can be used to model such plasticity (Reineking *et al.*, 2006), as well as the explicit representation of individual organs (Vos *et al.*, 2010; Yan *et al.*, 2004). The resource availability gradient can be easily represented as attraction field constraining the development of new organs. To balance the foraging and the exchange functions of the organ, and translate this function into a organ-specific phenotype, a reference point (delimiting the two functions based on the resource availability in the organ-local-environment) can be defined either as a function of the "niche" of the species, or relatively to the other compartment activity to ensure equilibrium. This change in function must be translated into a chemical and morphological function to fully reproduce the pattern, but this step is certainly challenging won't be discussed here.

This kind of implementation has the ability to capture foraging behaviour in environments where the resource can be scarce and highly heterogeneous, such as the shallow soils of mountain grasslands, with high fine grain heterogeneity (Deleglise, 2011; Reineking *et al.*, 2006). This spatially explicit plasticity should allow the emergence of competition patterns that cannot rise from the current implementation of the model. In addition to this emerging pattern, an organ-based plasticity should limit the phenotypic flexibility (see discussion in the subsection 1.1) and increase the phenotypic inertia, leading to stronger and more stable responses.

On the other hand, the implementation represents a technical challenge as it greatly increases the complexity of the agent, the decision rules and the overall computation cost of simulations. In the context of community dynamics, it seems such complexity would be more detrimental than beneficial. This complexity is also higher due to the increase in species-specific parameters to drive this architectural plasticity. It seems that progress needs to be done before considering such development at the community scale. However, imagining such an implementation lets us conjecture the effects of an alternative plasticity of the system and estimate the relative robustness of the results described above. This stability of the pattern emerging from the current implementation is discussed in the following paragraph of this subsection.

ARCHITECTURE PLASTICITY

2.3.2 Stress-based alternative implementations and robust observations

Aside from the way plants alter their phenotype to respond to estimated heterogeneity (spatial and temporal) in resource availability, the plasticity can also differ on how the estimation is built and modified during the time, and how it affects the plastic response. The results relative to the parameter filtering process (subsection 1.1) did not present the expected results in term of the amplitude of the response of the RSR to the watering treatment. Multiple factors can explain this behaviour, and multiple solutions have been mentioned. One of them is the stress-based plasticity that consists of model plastic behaviour as responses to stress, and to change the idea of memory into a sensitivity variable. This idea develops the concepts established by the biological understanding of the plasticity of the article from Crisp *et al.* (2016). They present the molecular mechanisms that can be involved in the memory or recovery of a stress event, *i.e.* how the plant capture the change in condition and how this information is stored (or not). As illustrated in the figure 2.29, after a stress the plant can recover and return to the pre-stress expression (return to the default phenotype) (Liu & Stützel, 2004), or maintain the level of expression (stress response phenotype) (Peterson & Billings, 1982). If it recovers, it can maintain the memory of the stress and have an amplified response or reset and ignore the event, leading to a similar response during the second stress.

STRESS-BASED PLASTICITY

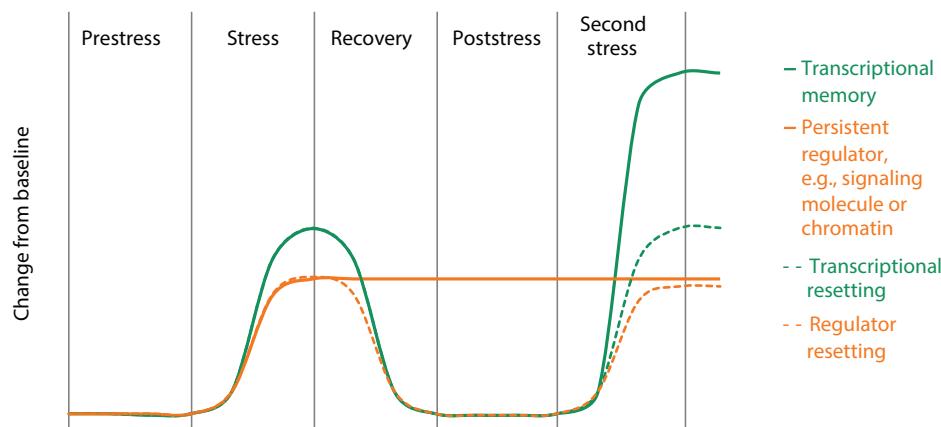


Figure 2.29: Stress memory and recovery. A theoretical example of memory formation, where up to thousands of stress-inducible transcripts (green lines) respond to the initial stress, concurrently with an accumulation of signalling molecules and the release of repressive chromatin (orange lines). Upon reexposure to a second stress, persistent signalling molecules and a retained accessible conformation of chromatin (solid lines) allow an enhanced stress response. The recovery period is a critical window where plant memory can be consolidated or resetting (dashed lines) can occur. Modified from Crisp *et al.* (2016), see the paper for more details.

Such mechanism would stabilise the plastic responses in case of non-recovery, or increase the inertia and the amplitude of the response with the transcriptional memory. The stress can be quantified easily, leading to a proportional response of the phenotype to compensate for the stress. In the context of the functional equilibrium, the deficit in the activity in one organ can be compensated by its increase in exchange area. Because the response is related to the stress and not a gain function, it does not have to follow the same constraints as the initial strategy as it is in *MountGrass*, offering a response decorrelated from the resource-use strategies. When the response can be achieved in multiple ways (increase in allocation or morphological change), a decision must be developed. It seems that this functioning allows for the integration of multiple stress factors, however, difficulties may emerge if they alter the same organ. Cases of additive stress (water and nutrient) can be observed in empirical studies (Fort *et al.*, 2015), suggesting that an additional approach to this problem could work.

Multiple stresses integration (Pierik & Testerink, 2014) was one of the objectives of the model *MountGrass* and it was integrated but not tested.

The implementation of the stress-based plasticity seems to have the potential to better mimic the plastic behaviour of plants, with recovery and amplified responses, reduced constraints on the axes of the plastic response and greater response variability. However, it comes with an additional level of complexity with more required species and stress-specific traits, and stress-specific decision rules.

As mentioned, the implementation of stress-based plasticity requires new decision rules to drive the trait response to specific stress as there are no longer controlled by an integrative gain function. Reaction norms used to characterise the plastic response of traits along a gradient constitute the perfect tool to drive such plasticity. An ambitious implementation that would distinguish the plastic responses of different species could maintain a general pattern with a shared formula of the reaction norm, but with different parameters between species.

Because the reaction norm approach does not give an optimum phenotype, but a variation of the current one, default phenotypes must be defined. Considering that these default phenotypes are viable, they should benefit from a more stable plasticity. Indeed, the plasticity based on a gain function targets one optimum phenotype considering the estimation of conditions at a given time. Therefore, it does not consider neither the probability of having wrong information and as a consequence, a non adapted phenotype nor the temporal variability that would require changes in phenotype not possible in a given context or time-frame. On the other hand, reaction norms are able (because they are less constrained) to produce plastic responses that are more stable (even if less performing in stable estimated conditions).

The reaction norms, as opposed to the integrative shared gain function, allows a great heterogeneity in plasticity. This plasticity seems necessary when the plastic responses of multiple species along multiple gradients are observed. Indeed, different species may respond differently to specific treatments (Freschet, Bellingham, *et al.*, 2013; Grassein *et al.*, 2010), or even different populations (Frei *et al.*, 2014), or along a large gradient (Kichenin *et al.*, 2013).

While the implementation of species-specific reaction norms allows contrasted responses, these plastic responses need to make sense in an ecological perspective. In other words, the alternative changes in phenotypes need to lead to a greater (or more stable) fitness. Therefore, in face of a stress, to maintain positive fitness ones can either try to avoid the stress or try to resist to the stress. It is often hard to tell which strategy is the best (and it may depend on the overall resource-use strategy of the species), therefore they coexist and be observed between different species in the same conditions (Pérez-Ramos *et al.*, 2013), or alternate if the conditions offer sufficient information to determine which strategy is the better (Heger, 2016). Under stress-based plasticity, the form and parameters of the reaction norms can control the balance between the two. Under architectural plasticity, the direction of the response to the stress can also allow these contrasting responses to coexist (reduction of the non-limiting-organ exchange area, or an increase of the limiting-organ exchange area).

Having described roughly two alternative/extended implementations of the phenotypic plasticity, we can try to estimate if the results observed with the cur-

REACTION NORMS

RESISTANCE OR AVOIDANCE

ROBUST OBSERVATIONS?

rent implementation would be reproduced under these alternative models. This should give us an idea of how these patterns can generalise.

In summary, two alternative implementations are proposed:

- I1: the architectural plasticity, exchange area regulation based on measure difference in activity;
- I2: the stress-based plasticity with species-specific additive reaction norms.

The main effect of plasticity is increasing the niche width and the niche overlap. Also, without plasticity costs, the plasticity tends to reduce the fitness differences between species. The architectural plasticity should give similar responses to changes in resource availability, even if there is optimisation function. Because the response is driven by the relative activity of the organs, equilibrium should be maintained in most cases. Because all traits respond to modify the exchange area of the two organs, the risk of lag should be limited. But, this can also be translated into rapid exhaustion as discussed for the plasticity implemented in *MountGrass*. Both forms of gain should be reproduced in this the implementation I1. In addition, the architectural plasticity provides a solution for a more efficient foraging that can further increase the potential productivity, the competition intensity (Maire *et al.*, 2013) and even lead to differentiation (Roscher *et al.*, 2015).

The alternative implementation I2 should also provide niche widening and fitness difference reduction, but the reaction norms should avoid exhaustion mechanisms, especially if they authorise a convenient shift between stress avoidance to stress resistance strategy under increasing stress intensity. The reaction norm implementation is closer to natural behaviour by an implementation inspired by molecular mechanisms rather than evolutionary hypothesis. Therefore the chances of maladaptive plasticity to emerge are greater because there are no constraints for a coordinated plant functioning. This would be particularly the case if the reaction norm forms and parameters are defined thanks to evolutionary approaches in conditions different from the tested conditions (due to global change for example). Because these two forms of plasticity should prevent unbalanced plant functioning, the asymmetry in the gain in variable conditions should be preserved.

The current implementation present the simple and coherent framework that allow to simply explore broad effects of the plasticity on the community. The implementation I1 offers a great tool to explore the effect of the plasticity on the fine scale and how these fine-scale interactions may shape the community functional diversity. The implementation I2 can better be used to explore the dynamics of plasticity strategies. Overall the two alternative implementations should present similar broad effects on the community properties, and the conclusions of this work can be generalised. All implementations present interesting particularities that can be used to explore different questions.

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V

COMMUNITY DYNAMICS

This second result chapter examines the effects of the phenotypic plasticity at the scale of the community. Another parameter filtering processes is performed and described in the first section of this chapter. The second part focuses on the effects of the plasticity on the main properties of the community. The impact of the plasticity on species diversity is particularly investigated. This chapter gives a glimpse of the potential of the model to answer various questions around the role of intraspecific variations on diverse community properties.

1 COMMUNITY LEVEL SIMULATIONS: NON PLASTIC COMMUNITY

1.1 Parameter filtering

1.1.1 Method

Weather data for the time period between 1959 and 2014 has been computed by the MeteoFrance model SAFRAN by Déborah Verfaillie using GPS coordinates, slope, azimuth and horizon computed from a digital elevation model. These parameters were also used by the model CROCUS to compute the snow accumulation and the snow melting. These high frequency data (resolution under 1h) have been averaged on a daily time-step and used to compute input variables for *MountGrass*. The snow in particular defines the length of the growing season starting with the first snow melt of the year and finishing the day of the first snow fall during the autumn or winter. The simulated years above 2014 are randomly sampled from the existing dataset between 1995 and 2014.

WEATHER DATA

The six sites have been chosen to test the consistency of the parameters, and open the door to the exploration of the effect of the climatic variables. This last aspect is not developed in this manuscript.

A community level parameter filtering is conducted for a new table of parameter sets. The tested parameter sets are composed of all the parameter sets accepted at the individual-scale with 50 randomly sampled among the rejected parameter sets. They are completed with five community-level parameters: seed germination density, drought mortality, ageing mortality, plasticity cost for environmental sensing and plasticity cost for trait changes (see chapter 4 for details). The values of these community-level parameters are randomly sampled with a LHS procedure.

PARAMETER FILTERING

The simulations run over 300 hundreds years for 6 sites with similar soil depth, but contrasted climate, on squares of 2,500 square centimetres, under *non plastic* allocation algorithm. After a stabilising phase of 50 years, the simulation is stopped and the parameter set rejected if no individual persist and the seedbank is empty. The seedbank is composed of seeds contained in the seedbank and seeds from the metacommunity. The total of seeds is defined by the seed germination density and the area simulated. The seeds from the simulated community

SIMULATIONS

represent up to 80 % of the seedrain, less if the seed production is limiting. 400 species compose the meta-community with traits randomly sample from distributions estimated from the accepted parameter sets at the individual scale. More complex procedure could be imagine to better take benefit of the information extracted from the individual-level calibration. This method is preferred because only one species is evaluated for each parameter set at the individual-level, thus no distribution specific to each parameter set could be used. This method still allows to avoid traits values that make no sense in any of the parameter set and reduces, even marginally, the number of potential non-viable species.

1.1.2 Results

Among the tested parameter sets, only 77 were selected after the parameter filtering process.

PARAMETER FILTERING

Because too few parameter sets are selected with contrasted parameter values, no sensitivity analysis could be conducted to determine the key parameters of the model. For the same reason, the parameter effects are not detailed.

GENERAL BEHAVIOUR

While the main properties of the simulated communities are explored in the following subsection, the general community growth can be observed for these simulations. The individual profiles show a relatively high variability within the season, that is coupled with high inter-site and/or inter-seasonal variability for any given parameter set. Despite variable growing-season starting dates, and some variability within parameter sets, the smoothed-profile show a consistent behaviour. This pattern is characterised by two distinct growth periods: (1) the initial growth corresponding to the use of the stored resources, then followed by the growth promoted by the favourable conditions of the spring and early summer, and (2) another growth period at the end of the summer/autumn, following the growth reduction of the mid-summer. Two peaks can be observed during the first phase, but the first one is only noticeable for a few conditions where the season started early.

1.1.3 Discussion

The parameter filtering process deployed here is sufficient to select viable parameter sets allowing stable simulations. Ones could develop extended calibration plans to stabilise the behaviour of the model and ensure more realistic output. However, such approaches are mostly interesting when the model is built to infer information about specific, well described systems, instead of qualifying the general effect of freshly modelled mechanisms. The non reduction of the analysis of the model to one parameter set also increase the confidence in the observed pattern, and the conviction that they emerge from its structure rather than specific parameter interactions. Moreover, ambitious calibration procedure should rather be reserved to mature models, from which the general responses are well described and understood.

PARAMETER FILTERING

The biomass profiles of the simulated communities show both consistency in the growth pattern, and high daily variability. The variability observed highlights the great the sensitivity to the weather variables. This sensitivity certainly favours positive effects of the phenotypic plasticity, if the changes in phenotype are responsive enough and do not suffer from a lag.

DRIVEN BY THE WEATHER

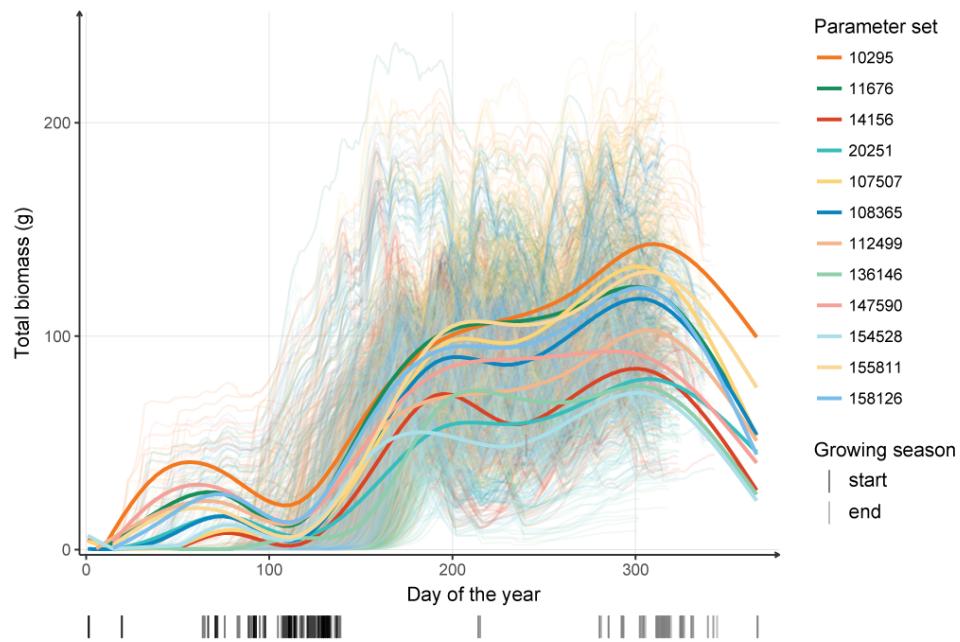


Figure 1.1: Total biomass over time during the growing season for the *non palsticallocation*. The thin lines illustrate the individual seasons profiles ($n = 20$) for different sites ($n=6$) and parameter sets (colour). The growth profile of the different parameter sets are estimated with GAM models. The marks at the bottom indicate the beginning and the end of the seasons.

The consistent growth pattern with two distinct growth periods correspond to field observations where plants are generally divided between early flowering, matching the first biomass peak, and late flowering corresponding to an autumn growth and reproduction. This coherent behaviour, driven by the climate, gives confidence in the integration of the climatic variables as drivers of the community. Further work could be done to confirm the respective role of the temperature and precipitation, but this work focuses on the effect of phenotypic plasticity and both the relative sensitivity to the daily variations in the conditions and the importance of the climatic variables as driving forces supposes that the plasticity has the potential to affect the mountain communities.

The parameter filtering at the community scale ensure stability of the simulations at the community level. It also gives confidence in the global behaviour of the model, and in the driving role of the climatic variables.

2 PLASTICITY: IMPACT ON SPECIES FITNESS AND DIVERSITY

After a simple parameter filtering, guaranteeing the stability of the communities, the effect of the plastic allocation algorithms can be investigated at the community level. In a similar way as the previous section, the focus is given to the main properties of the community: the diversity, the productivity and the identity.

2.1 Plasticity and diversity

2.1.1 Method

To test the effect of plasticity on coexistence and community dynamics, runs from the parameter filtering are used as starting points to limit the simulation time of the stabilisation phase. For each parameter set tested, 6 different sites were tested during the calibration phases, 77 parameter sets were accepted and a sample of 18 parameter sets were tested, resulting in 108 communities. Each of those is the starting point of three parallel runs that differ only by the allocation algorithm used: *non plastic*, *fixed-equilibrium* and *plastic-optimisation*. The *fixed-equilibrium* is favoured to *fixed-optimisation* algorithm because previous part of the document focused on this algorithm and because it is simpler to analyse. The *plastic-optimisation* algorithm is simulated despite the relatively poor performance results observed in constant conditions and the high convergence. This is justified by the introduction of plasticity cost, continuous species specific plasticity ($0 < \tau < 1$) and temporal and spatial heterogeneity that should mitigate the negative sides of this allocation mechanism and give information of processes at stake.

SIMULATIONS

The plasticity costs (maintenance: related to the value of τ , and displacement: relative to changes in phenotypes) defined in the parameter sets are applied to all algorithms. In the *non plastic* simulations, this results in an artificial additional cost to all species, especially those with a low value for τ , but with no potential gain from plasticity as the allocation is non plastic. This choice was made to ensure that the differences between the simulations are the results of the allocation algorithm only, and not a cumulative effect of the algorithm and the plasticity costs that could not be disentangled. This artificial cost can be seen as an artificial abiotic filtering process. Because 400 species are present in the meta-community, enough species with high values of tau should be able to invade the habitats, limiting behaviour emerging from low sampling.

To allow comparison between the datasets, the variables are normalised over the mean value of the variable under *non plastic* allocation. So the *non plastic* algorithm is the reference, but the variability caused by sites and seasons is still visible.

NORMALISATION

The normalisation $Vn_{a,p,t,s}$ of the variable V for the allocation algorithm a , the parameter set p , the time t and the site s is given by the following formula:

$$Vn_{a,p,t,s} = \frac{V_{a,p,t,s}}{\bar{V}} \quad (2.1)$$

$$\bar{V} = \frac{\sum_{a==\text{non plastic}} Vn_{p,t,s}}{n} \quad (2.2)$$

where n is the number of observations for the *non plastic* algorithm.

For practical reasons the entire composition during the season are not stored during the simulation process. The trait values are estimated *a posteriori* from the reproduction pool composed of living individuals and seed produced. The species default values are used to compute the community weighted mean of traits with the living biomass or the cumulative seed biomass. Therefore, even if under *plastic-optimisation* allocation the plants can change their trait values, these changes are not measured.

SPECIES & TRAIT VALUES

The diversity indexes are computed from the reproduction pool (defined above). The *alpha* diversity is simple expressed as the mean number of species per site and per year. The *beta* diversity is defined as the total number of species divided by the *alpha* diversity minus one.

The abundance ranking is computed from the reproduction output, under the hypothesis that the reproductive output is proportional to the realised abundance and constitute a good proxy for the fitness.

2.1.2 Results

The level of coexistence is evaluated by the number of distinct species that manage to maintain at least one individual or produce at least one seed at the end of the season. This criterion allows to ignore the potential non stable diversity introduced by the meta-community invasion (sampling of species in the meta-community pool) and to consider species that can be filtered out due to seed mortality. The number of species increases in almost all simulated years and sites for both plastic allocation algorithms, with a median of 1.5 times the number of species in *non plastic* simulations (see figure 2.1.2). This factor can go up to 6 for *fixed-equilibrium* and 9 for *plastic optimisation*.

The effect of plasticity on coexistence is driven by the benefits of plasticity at the individual scale. These benefits are mitigated by the cost of plasticity, particularly the maintenance cost that affect all species relatively to their potential plasticity (proportional to $1 - \tau$).

Low values of plasticity maintenance cost (see figure 2.2) show higher diversity for both plastic allocation algorithms. This trend is consistent across sites despitely some inter-annual variability in the diversity. The effect is a bit less stronger for *fixed-equilibrium* than for *plastic-optimisation* (as already observed in figure 2.1.2). It is also important to notice that the cost of the plasticity has no negative impact on the coexistence levels for *non plastic* simulations.

The mechanisms through which the phenotypic plasticity impacts species richness are multiple (see figure 3.7 in chapter II). However it is hard to disentangle them all.

The plant density can be affected by the phenotypic plasticity leading to higher species diversity (Lepik *et al.*, 2005), leading to the sampling of more numerous species. The density, estimated by the number of individual after the reproduction phase (persisting individuals and produced seeds), is consistently higher in *plastic* simulations (data not shown, but see figure 2.3). But the difference is relatively low (around 3% higher than the *non plastic* median density) and an order of magnitude lower than inter-annual and inter-site variations that can go up to 40% difference relative to the median density (for any given parameter set). Moreover, the species richness shows no evident relationship with the density of plants in any of the algorithms (see figure 2.3). In addition, the number of individuals is greatly depending on the seed input parameter (strong linear correlation), but this parameter has no consistent effect on the species richness (data not shown).

The productivity may also be impacted by the phenotypic plasticity at the community level. Multiple mechanisms can be involved, but in any case a higher productivity is achieved by a higher efficiency in the use of the resources given. The plasticity can affect this efficiency at the individual level (with positive ef-

DIVERSITY MEASURES

EFFECT ON COEXISTENCE

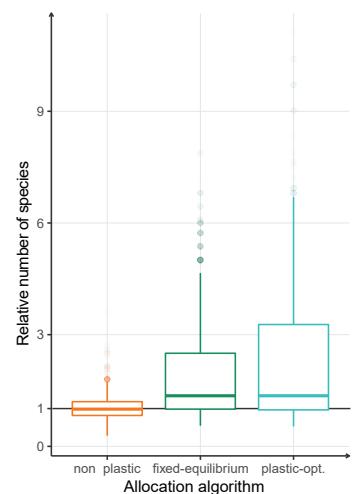


Figure 2.1: Relative species richness in the three plasticity treatment. To negate the variability due to the parameter sets, the realised number of species is divided by the median number of species in *non plastic* treatment for each parameter set. The variability is due to random invasion and climatic variability (inter-sites and inter-seasons).

PRODUCTIVITY

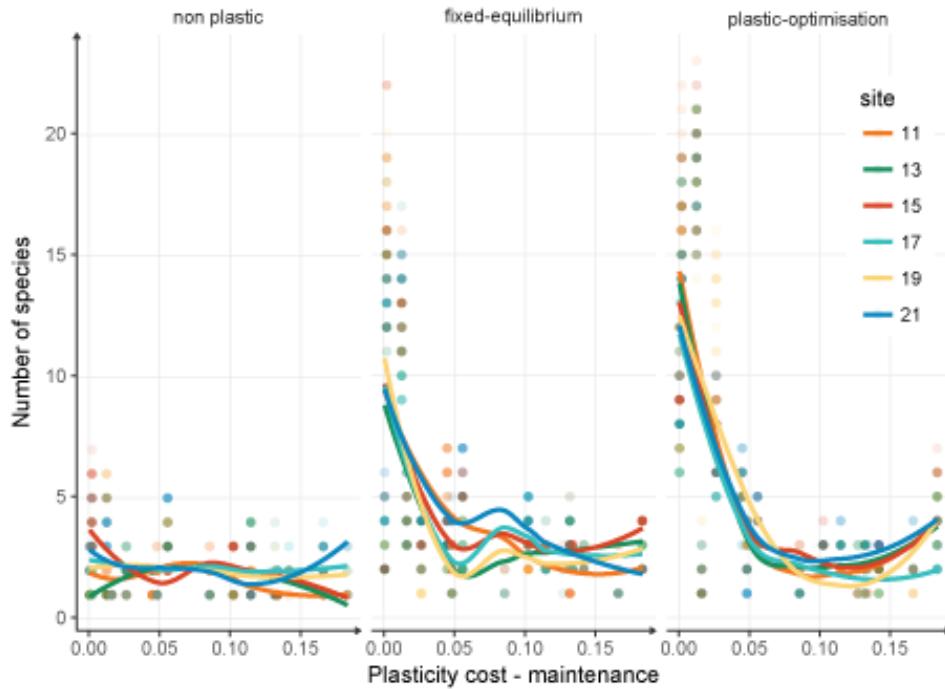


Figure 2.2: Effect of the cost of plasticity-maintenance on the absolute number of species in the three plasticity treatments. Individual season values (points) and site-specific trends (gam smoothing line) are represented.

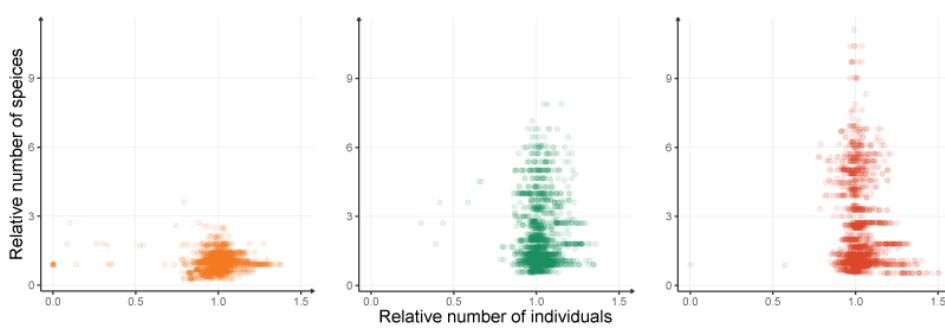


Figure 2.3: The species richness against the plant density for the three plasticity treatments. To negate the variability due to the parameter sets, the variables are divided by the mean value for the *non plastic* treatment for each parameter set.

fects as observed in section 2) or at the community scale with changes in the dominant species, plant density and competition intensity.

The productivity of the *non plastic*, *fixed-equilibrium* and *plastic-optimisation* allocation algorithm show little differences. The *non plastic* simulations average biomass tend to be a bit higher in certain cases. Like the diversity and density, the normalised yearly average are used to do the comparison, but the average biomass does not show great variations between plasticity, with a higher variability between sites and seasons. *Non plastic* and *fixed-equilibrium* median are quite similar, and the *plastic-optimisation* show lower productivity than the other two algorithms. Both the conserved average plant biomass and the constant plant density lead to a constant community net productivity.

The allocation algorithm is expected to alter the fitness of potentially plastic plants. The selective effect of the allocation algorithms is investigated by plotting the τ value of species that are maintained in only one of the algorithms (in figure 2.1.2). Because of the plasticity cost, the selection of species with low values of τ signifies an improvement of the fitness due to plasticity. The distribution of τ is fairly high for *non plastic* species and almost 75% of the species have a value above 0.8, whereas *fixed-equilibrium* specific species have lower values ranging from 0.2 to 1 with the median around 0.7 and the *plastic-optimisation* species have even lower values with a median around 0.55.

There is a selective effect of the allocation algorithm on the axis related to the plastic strategy, but the resource-use strategies could also be impacted.

After the productivity and the diversity, the identity of the communities is investigated.

The mean and median values of the CWM of the resource-use strategies (PAR and PAS) do not show any shift between non plastic and fixed-equilibrium algorithms (table 2.1). The strategy variability is lower for the root strategy, than for the shoot strategy. The variability is relatively high compared to the differences between the two algorithms. The plastic algorithm show low values for the mean and median, with high variability.

Root strategies show high values (around 0.8) of active tissue allocation is all algorithms, in contrast with lower values of the shoot allocation of active tissues (around 0.6).

Unlike the diversity, the identity of the community, defined by the dominating species, does not show a clear shift under plastic allocation. The great variability observed for each algorithm can be easily decomposed and explained because it is linked to the community structure and the dominant species. To decompose this variability in the identity, the community weighted mean To analyse this variability, the community weighted means (CWMs) for the proportion of active tissues in roots (PAR) is visualised along time for the 6 sites, for 5 representative parameter sets (see figure 2.7). The variability is decomposed between the spatial and the seasonal variability. Under *non plastic* allocation, the CWM values

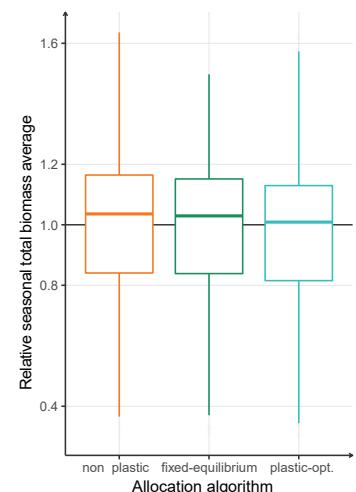


Figure 2.4: Average total biomass relative to *non plastic* simulations, in the three plasticity treatments. To negate the variability due to the parameter sets, the variable is divided by the mean value for the *non plastic* treatment for each parameter set.

PLASTICITY: A WINNING STRATEGY ?

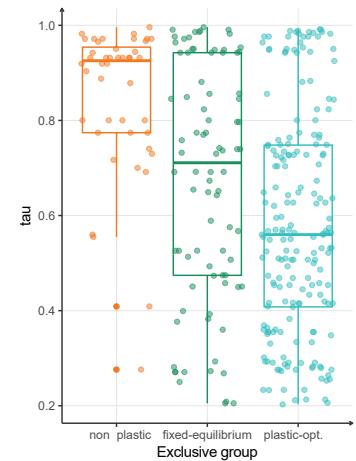


Figure 2.5: Plasticity levels of species that are present in only one type of plastic treatment. Each point represent one distinct species.

VARIABLE STRATEGIES

Variable	PAR			PAS		
	Mean	Median	SD	Mean	Median	SD
Non plastic	0.801	0.823	0.0733	0.644	0.657	0.152
Fixed-equilibrium	0.804	0.823	0.0714	0.653	0.657	0.143
Plastic_optimisation	0.749	0.778	0.133	0.589	0.600	0.200

Table 2.1: Summary statistics (mean, median and standard deviation (SD)) of the community weighted-mean of resource-use strategies in root (PAR) and shoot (PAS) for the three main allocation algorithms.

for PAR are stable during time, but contrasted between sites. In contrast, under *fixed-equilibrium* and *plastic-optimisation* allocation, the temporal variability is greater, but the site specific means are closer. This pattern is reproduced for the shoot resource-use strategy (data not shown).

The differences in community structure certainly explain these contrasted source of variability of the community identity. The structure is altered by the increased species richness under plastic allocation (see figure 2.6), leading to a reduction of the abundance of the most dominant species, in addition of a long tail of the rank-abundance curves due to numerous species with low abundances.

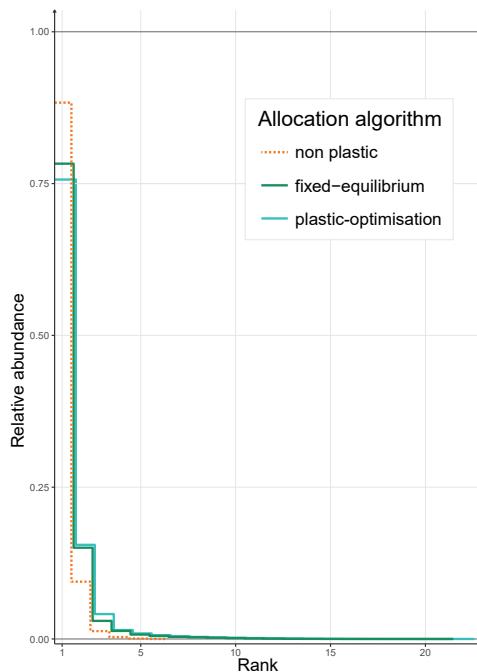


Figure 2.6: Rank abundance curves for the *non plastic* (-·-), *fixed-equilibrium* (-) and *plastic-optimisation* (-·-) algorithms. They illustrate the structure of the communities highly dominated by one species in *non plastic* simulations, and highlight the long tail of rare species in plastic communities.

This shift in structure at the community scale, but also at the meta-community scale suggest a strong effect of the allocation on the overall structure of the ecosystem.

Introducing plasticity in allocation leads to a shift in the diversity types. *Non plastic* simulation tend to have more differentiated sites, captured by the high values of *beta* diversity, but with low *alpha* diversity as previously discussed (see figure 2.8).

The total amount of species present over all sites and all seasons also varies between allocation algorithms, with a average total amount of 4.26 (median 4) for *non plastic* allocation, of 7.69 (median 5) for *fixed-equilibrium* allocation, and of 10.1 (median 4) for *plastic-optimisation* allocation.

DIFFERENT DIVERSITIES

2.1.3 Discussion

The great increase in the species richness observed under plastic allocation, for both the *fixed-equilibrium* and *plastic-optimisation* algorithms, results from a reduction of the strength of the filters. The results at the individual level analysed in the previous part suggest a weakening of the abiotic filter (1) as the importance of the plastic dimensions is reduced (static gain) and (2) variability in conditions can be overcome reducing the phenotype sensitivity to changes in resource bal-

FILTERING

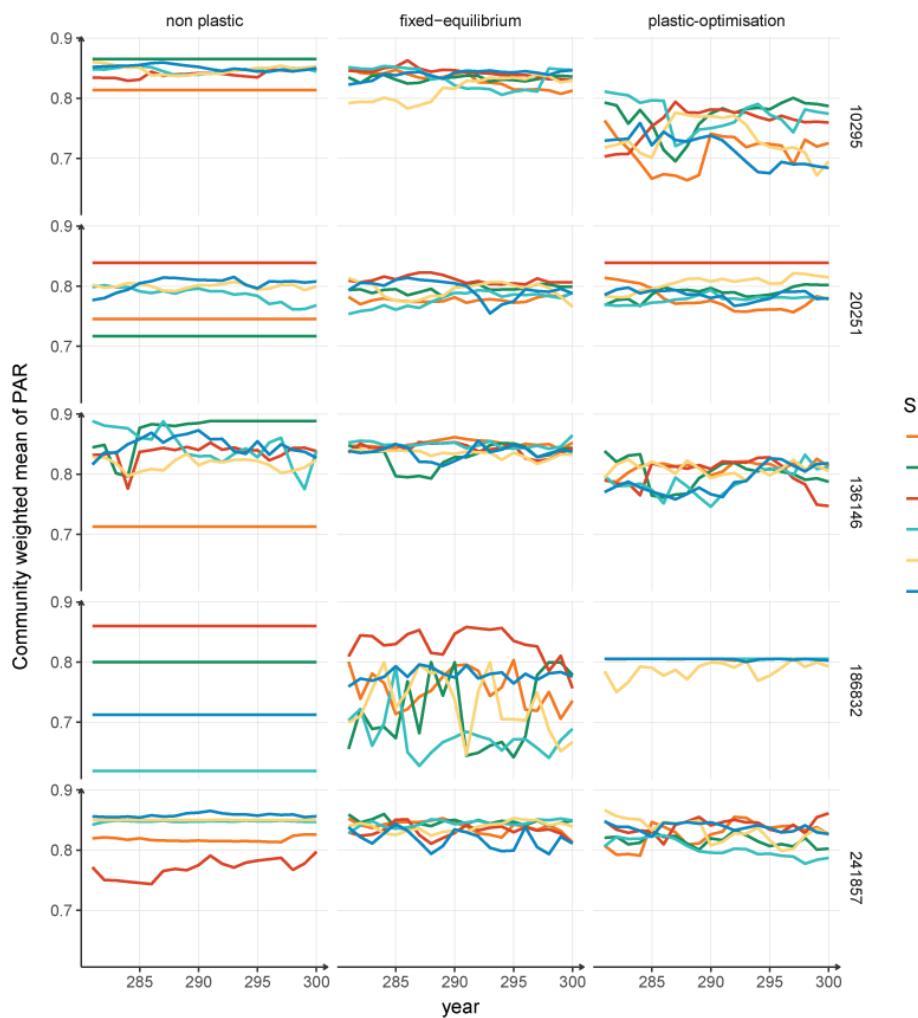


Figure 2.7: Community weighted means of the proportion of active tissues in roots for each site, as a function of time and the allocation algorithm, for 5 representative parameter sets.

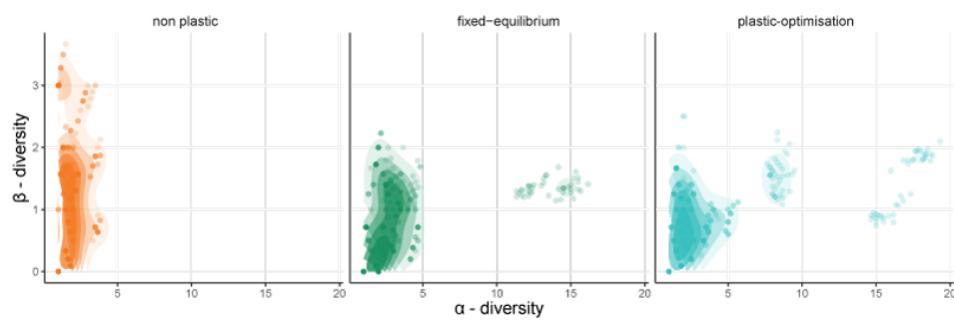


Figure 2.8: *Alpha* and *beta* diversities as function of the allocation mechanism.

ance (dynamic gain). In the other hand, the reduction of the abiotic filtering was anticipated to increase the competition intensity as more plants can settle in a given habitat. The reduction of the fitness differences observed at the individual level may explain a reduction of the competition exclusion despite a increase in the competition intensity. However it is relatively difficult to quantify the relative importance of competition relative to the abiotic filtering as they both are they both alter the resource levels. The overall reduction of filtering suggest a greater importance of the abiotic filtering reduction compared to the increase in the competition exclusion.

The absence of changes in the plant density, together with the stability of the community productivity, support the idea that if the abiotic filtering is reduced, it goes with an increase in the competition intensity. Therefore, the increase in species diversity is explained by a shift from a non uniform abiotic filter, to a more uniform biotic filter. Better understanding of the interactions between species strategies, and how they are modulated by plasticity could help building such interpretations at a higher level based on existing theories (Chesson, 2000b). With this perspective from the coexistence theory, we could explain the high diversity by the effect of the plasticity as an equalizing mechanism. Phenotypic plasticity, by allowing species to converge toward better phenotypes or to resist stresses, maintain a certain fitness evenness between species favourising the coexistence. Also, while these species are maintained, stabilizing mechanisms such as intra-specific competition can play a bigger role. However, while the intra-specific competition is recognised as often more important than the inter-specific competition (MacArthur & Levins, 1967), the resource-use strategies as they are implemented in *MountGrass* have certainly hierarchical effects (Kunstler *et al.*, 2016) as some strategies are dominant in certain conditions. Establishing how the intra- and inter-specific competition balanced, *i.e.* if limiting similarity or competitive dominance prevail is crucial to better understand the community assembly in this context. This aspect is also critical because plasticity can affect this balance as observed by Bennett *et al.* (2016). The current implementation of *MountGrass* offers specific functions dedicated to paired simulations to evaluated the competitive and facilitation interactions. This tool can also be used to determine the transitivity properties of these interaction that can affect the ability of the model to maintain stable coexistence (Levine *et al.*, 2017).

Finally, the fact that the species richness is not altered by the cost of the plasticity for *non plastic* simulations (making certain phenotypes non viable), but is altered under plastic allocation, supports the fact that the species richness effect results from the allocation algorithm rather than the plasticity cost.

As mentioned, the productivity is mostly conserved between the allocation algorithms, as well as the plant density. I hypothesise that the increase in competition compensates the static and dynamic gains provided by the plasticity. It suggests that under *non plastic* allocation, the carrying capacity of the sites is reached and that it cannot be exceeded despite the potential increased efficiency provided by the phenotypic plasticity. Because there is no change in the mean density, the mean resourcec-use efficiency at the scale of the plant should be similar. As analysed in the previous section, the plant efficiency can be limited by: the individual organ-specific efficiencies, the unbalance between organ activities or the resource use general level. Disentangling the component of efficiency should allow to better understand the limits of the productivity. The plasticity may have

PRODUCTIVITY & DENSITY

a greater effect on the plot productivity under specific circumstances of strong disturbances, thanks to a higher resilience to drought or grazing events (Maire *et al.*, 2013). On the other hand, it could be that the increase in competition leads to a decrease in resource-use efficiency as explained by the game theory (Farior, 2014). But the absence of clear differences in resource-use strategy does not support this hypothesis.

The density of plant is also unchanged. This is consistent with the stability in productivity. This stability in the plant density eliminates any sampling effect that could explain an increase in the observed species number for a given plot area as observed in Lepik *et al.* (2005).

Individual level results suggest the importance of the resource-use strategy for the success of the growth in different conditions. This idea seems to be validated by the observation that different species dominate different sites under *non plastic* allocation. However, this pattern disappear under any of the two plastic algorithm tested. Thus, the root-shoot balance is probably more important in the selection of the success of the species.

DOES IDENTITY MATTER?

Considering the variability of the weather during the season, the asymmetric dynamic gain should have promoted more exploitative species under plastic allocation. However, no convincing differences can be detected between the average CWM resource-use strategies between *non plastic* and *fixed-equilibrium* algorithms, for shoots or roots. This surprising result suggests that the differences in dynamic gain between strategies are not large between the different strategies. This result could also be explained by the stronger effect of the RMF axis (compared to the PAR and PAS) that lead to a low sampling of the other axis and hide potential effects of small amplitude. This effect can be exacerbated by the strength of the trade-offs (already noted in the previous chapter) that limits the number, and thus diversity, of viable strategies. This problem also limits our ability to interpret the differences between shoot and root successful allocation strategies to active tissues, because they may results from strong parameter effects rather than a difference in the sensitivity of the two organs. Similar experiences as in the previous chapter (analysis of the best strategies along a gradient), but including shoot strategies may enable us to compare the relative importance of the two activities in the context of community simulations.

The *plastic-optimisation* algorithm shows lower values for shoot and roots proportions in active tissues. However, because the values use to compute the CWMs do not take into account the plasticity in these traits (for technical reasons, the expressed trait values are not recorded), this difference is artificial and does not reflect changes in the dominant strategies.

The detection of the plasticity effect on the community identity can also be masked by changes in the structure of the communities.

COMMUNITY STRUCTURE

The increase in the species richness necessarily comes with a change in the community structure under plastic allocation. This shift consist in the reduction of the dominance of the most abundant species, an increase in the second and third dominant species, as well as a longer "tail" with many species of low abundance. While the presence of numerous low abundance species could suggest marginal effects of the plasticity allowing the maintenance of rare species at the border of their niche, the reduction of the relative abundance differences between the species dominating the community demonstrates a stronger effect.

This strong effect of the plasticity on the community structure explains the differences in identity variability under the two types of allocation algorithms. On one hand, under the *non plastic* allocation, the identity varies mostly between sites, but stays fairly stable between seasons. On the other hand, the variability is temporal rather than spatial under *fixed-equilibrium* or *plastic-optimisation* allocation. Because the niches are narrow without plasticity, the small climatic differences between the sites lead to different compositions and high spatial heterogeneity in the community identity. The strong filtering force that constitute the changes in conditions does not allow species at low density to establish. The extinction of these species releases the competition intensity after a climatic stress event, offering more resources for the dominating species that translates into a large reproduction effort. Because of storage effect, and strong abiotic filtering, the dominant species is favoured even in bad years. The combination of the sensitivity of the fixed phenotypes to changes in conditions with population dynamics favours stable low diversity communities. Under plastic allocation, the niches are wider, allowing more species to invade and survive a given habitat, despite changes in conditions. Because they have wider niches, and the climatic conditions between sites are not that different, the chance that they invade multiple sites are higher than in *non plastic* allocation. Because more species are present, and the competition is more even, the seasonal variations in conditions allow changes in the relative abundance of the species while the community composition is stable. These changes alter the community weighted means and therefore the identity of the community. The differences in species composition and the effects on the CWM of PAR for the three allocation algorithms are illustrated in the figure 2.9.

The structural changes in the community and meta-community can be seen with the perspective of the diversity. While many diversity indexes could be used to decompose and analyse the diversity of such communities, these simple indexes (*alpha* and *beta* diversity indexes) are sufficient for this level of analysis and to express the differences in the structure of the ecosystem caused by the allocation algorithms.

The increase in *alpha* diversity has already been discussed and results from a niche widening (or a reduction of the abiotic filtering). The beneficial value of the plasticity to explain this increase in *alpha* diversity is demonstrated by the significantly lower value of τ for the species unique to one of the two plastic algorithms for each parameter set.

The lower total number of species over all sites demonstrates that the reduction of the *beta* diversity is explained only by the differences in *alpha* diversity. This interpretation is coherent with the conclusion that the niche overlapping induced by the phenotypic plasticity explains most of the community dynamics patterns.

The allocation algorithm is only one of factors that impact the response variables that are analysed in the previous sections. The parameter sets and climatic variables (year and sites for community-level simulations) also greatly impact the outcome of the simulation. While the perfect knowledge of the model and the total control over the simulations allow us to decompose and disentangle all these effect, the focus has been on the effects of the allocation algorithm, relative to the other effects. As mentioned in the method, the normalisation relative to

DIFFERENT FORMS OF DIVERSITIES

STATISTICS

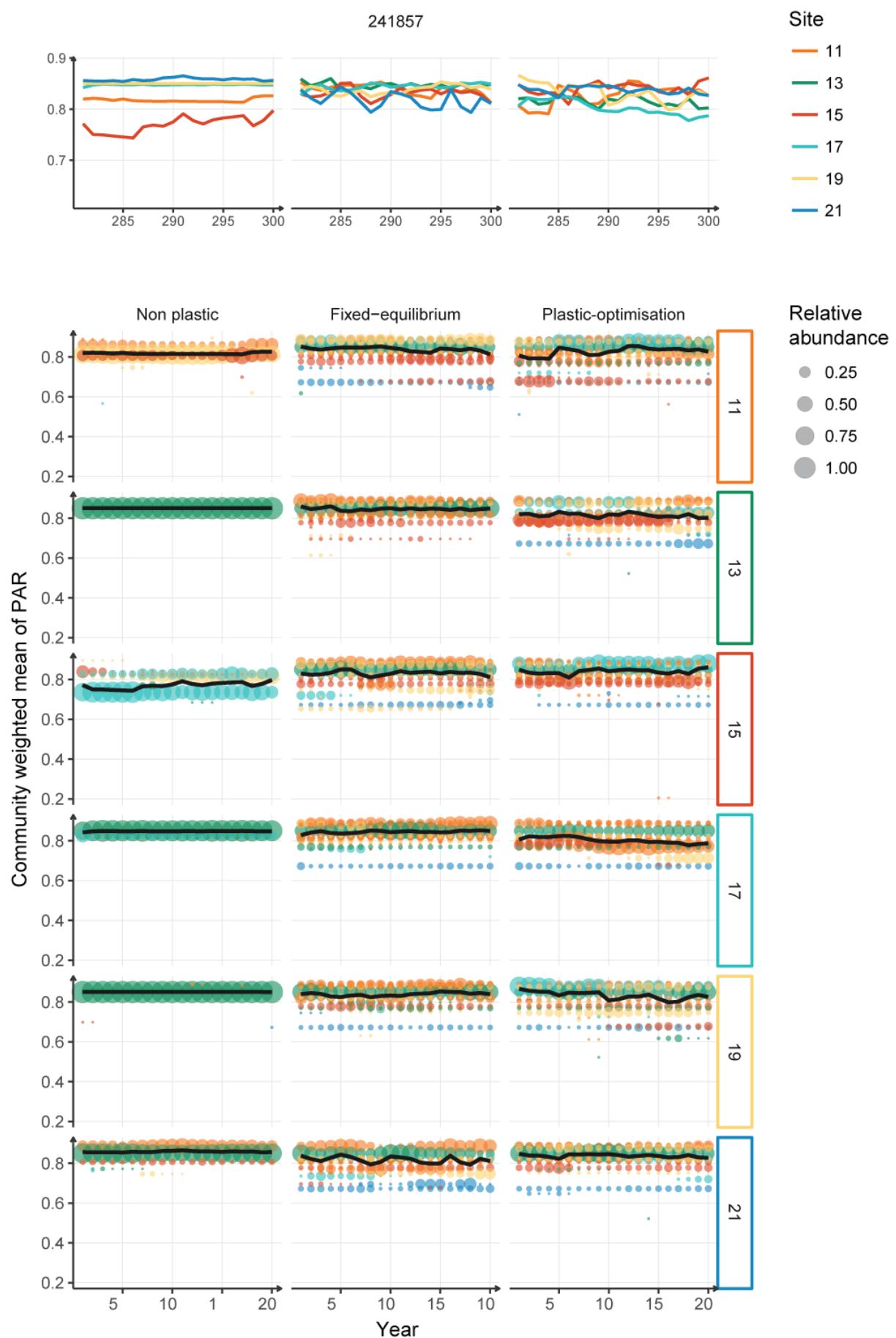


Figure 2.9: Inter-site and inter-season variability of the community identity (A) explained by the effect of the plasticity on the community structure (B).

the mean of each parameter set eliminates partially the complex effect of the numerous parameters on the scale of the variables, while keeping the overall behaviour (reduction, increase or stability). It also allows to compare the effect of the algorithm relative to the other factors source of variations (season and site). Maybe another normalisation could have been performed (standardisation), but this method seems to provide already consistent information.

One could regret the lack of statistical analysis to estimate the significance of the effects. But, as mentioned the total control and knowledge of the model would allow to ensure significance results for any test, and therefore is not informative (see White *et al.* (2014) for extended arguments). While the effect size could have been calculated, the graphical representations produced provide enough information to estimate these effect size and compare the effect of the explicative variable of interest (allocation algorithm) to the variability caused by the other factors.

I believe the representation of the model outputs through specific visualisations gives a better understanding of the general behaviour of the model, as well as an intuition of the unique differences between the different conditions, than large tables and statistical test could do in this context.

The introduction of phenotypic plasticity has many effects on community-level process, with consequences on the main properties of the communities (see figure 2.10). It reduces the filtering role of abiotic conditions, increasing the competition intensity, but it also decreases the fitness differences (or increases the competition fairness) leading to higher species diversity. The overall plot productivity does not seem to be affected by the allocation algorithm. This is explained by multiple factors: the absence of differences in plant density, similar resource-use strategies that maintain the overall tissue-efficiency, and the increase in competition intensity that compensates for potential increase in efficiency due to balanced activities. The identity was not impacted by the allocation algorithm, unlike the structure of the communities and meta-community, leading to a shift from *beta* to *alpha* diversity, and from inter-site to inter-season variability of the resource-use strategy.

PLASTICITY & COMMUNITY PROPERTIES

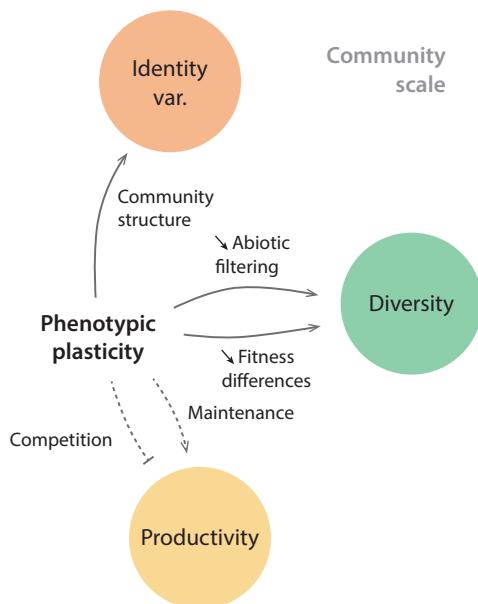


Figure 2.10: Effects of the phenotypic plasticity on the main properties of the community.

The simulation at the scale of the community produce surprising results. Imagining how stable these patterns would be under alternative implementations can give us an idea on how robust these results are. The two alternative implementations suggested are presented in the previous chapter.

ROBUSTNESS

On one side, the structure and diversity differences are explained by two main mechanisms: the reduction of the abiotic filtering and the reduction of fitness differences. The equilibrium architectural plasticity (I1) has the ability to maintain organ activity balance, while increasing the performance of foraging strategies. This efficiency (Maire *et al.*, 2013) guarantees the reduction of the abiotic filtering. The stress-based plasticity with reaction norms should also be able to reduce the abiotic filtering under the condition of the selection of sensible reaction norms. These reaction norms even have the potential to better stabilise the plant efficiency by regulating the overall plant activity, and not just the balance between the activity of the organs. On the other hand, the diversity is also promoted by the reduction of the fitness differences. The reduction of the sensitivity to changes in conditions partly explain this effect, but the convergence of the phenotypes also explains this reduction. While both alternative implementations should reduce these differences in fitness by reducing the sensitivity of the phenotypes to changes in conditions, the reaction norm implementation (I2) should limit the phenotypic convergence by the diversity of the reaction norms in presence. The contrasted strategies of avoidance versus tolerance should participate in the maintenance of functional diversity. This reduction of the convergence may limit the reduction of fitness differences promoting the coexistence (Chesson, 2000a). On the other hand, phenotypic plasticity may enable niche partitioning as observed in empirical data (Roscher *et al.*, 2015; Zuppinger-Dingley *et al.*, 2014). The beneficial effect of the phenotypic plasticity, because it is constrained by trade-offs allowing coexistence (Tilman, 2004), should favour coexistence in most conditions.

Both algorithms have potential for greater efficiency. This efficiency may affect the productivity in a larger way than the current implementation (Maire *et al.*, 2013). A finer exploration of the response of the community after disturbance events should give us better understanding of the effect of the plasticity on productivity stability (Richter *et al.*, 2012) on grassland systems.

Because the *alpha* diversity is expected to be impacted in a similar way than in the current state of the model, structural changes of the communities and meta-community are susceptible to be reproduced in the different implementations. The identity of the community, expressed as the CWMs for the resource-use strategies may however be impacted. Indeed, the impact of competitive species under architectural plasticity may be stronger, with either a rapid competitive exclusion of the subordinate species, or the rapid shortage in resources leading to more conservative species dominance. The reaction norm plasticity, by allowing more diversity in the plastic response may also have a drastic effect on the community identity. The complexity of the interactions and resource dynamics introduced by these implementations does not allow the anticipation of the effects on the community identity. At the contrary, it further encourages us to try alternative implementation of plasticity to unravel all these processes.

The plasticity as a strategy defended in the chapter III, that makes the plasticity an axis of strategic differentiation, is only superficially studied here. The figure 2.1.2 shows the average phenotypic stability value for algorithmic specific

STRATEGIC PLASTICITY

species (only reproduce in one of the algorithms). This results confirms that plasticity favours species with lower tau values. The particular relationships that may exists between levels of plasticity, the two distinct costs and the temporal variability of conditions should be investigated to better understand the role of the plasticity costs as a limit of the phenotypic plasticity (Auld *et al.*, 2009; DeWitt *et al.*, 1998).

The adaptative value of the different levels of plasticity can be measured by the distribution of the τ values against gradients of resource variability, allowing hypothesis testing on the limits of the plasticity.

2.1.4 A broader perspective on phenotypic plasticity at the community level

The strength of models as tools is to help us understanding the underlying mechanisms, but also to project the system of interest in alternative scenarios. While this subject is further discussed in the next chapter (chapter VI), the current results can still be analysis with this perspective.

SERVICES AND GLOBAL
CHANGE

The phenotypic plasticity effects at the community level mostly affect the community structure and diversity. The addition of multiple rare species, while they do not participate greatly to the productivity, they still provide numerous benefits. The species diversity can for example support a flower diversity that promote cultural services, as well as honey production. This flower diversity is also tightly linked to the pollinator diversity (Frund *et al.*, 2010) themselves enhancing the persistance of plant communities (Fontaine *et al.*, 2005). Such positive feedback mechanisms have essential positive feedback effect stabilising the coexistence.

The species diversity has multiple other benefits (see chapter II)(Tilman *et al.*, 2001). One of these effect is to enhance the stability of the community (Morin *et al.*, 2014). This effect is even more important in the context of the climate change. The shift in climatic conditions driven by the climate change may put some species outside of their fundamental niche. Such effect can lead to critical transitions (Scheffer *et al.*, 2001), especially in case of low diversity and narrow niches, where the equilibrium state is fragile. In this context, the phenotypic plasticity have two beneficial effects: (1) it widens the fundamental niche of the species, reducing the risk for rapid shifts, (2) increases the species diversisty, allowing subordinate species to become dominant (Adler *et al.*, 2006) with potential effects on community's stability. Also, while no net effects could be detected on the average productivity, the size of the seed rain may be affected, weakening the stability of the system and increase its vulnerability to plant invasion.

The modification of the meta-community can also have an impact of the response to global change. The high redundancy in species between site, while it decrease the *beta* diversity, also support the site stability. Indeed, in case of discriminated communities (communities are composed of unique and different species), any local transition leading to the local extinction of the species also leads to the extinction of the species at the meta-community level. Whereas, in redundant community structure, a local extinction can be reverse later thanks to invasion from undisturbed (or less disturbed) communities.

Redundancy and plasticity should also help smoother transition between states, and should allow management adjustment to be adopted. The poten-

tial effect on the resistance to alien species should also be investigated.

The development of this model also highlights the importance of the perspective on a phenomenon. One of the primary objectives of this work was to better understand the source and effects of intra-specific variability. This issue had received increasing importance (Albert *et al.*, 2011; Bello *et al.*, 2011; Siefert *et al.*, 2015; Violle *et al.*, 2012). And the question has been explored with empirical and statistical approaches (Bennett *et al.*, 2016; Jung, Albert, *et al.*, 2014; Jung, Violle, *et al.*, 2010), and theoretical models that allow the examination of the underlying processes (Hart *et al.*, 2016).

Theoretical models are great tools that allow, by the simplification of the problem and the identification and characterisation of the processes, to explicit the mechanisms and quantify emerging properties of the system by the study of their mathematical properties. Such an approach was developed by Hart *et al.* (2016) to investigate the impact of the intra-specific variability upon the coexistence mechanisms. They show an overall negative effect resulting from numerous processes. A part of the explanation, the Jensen's inequality effect with species interaction coefficient, might be overcome by the fact that empirical estimation of these coefficient should capture this effect. But another argument resides in the modification of the relative strength between the intra-specific and inter-specific competition interactions. While the reasoning is valid, it relies on an assumption, the symmetry of trait mediated competition. However, such assumption, deeply rooted in ecology (MacArthur & Levins, 1967) may not always be verified (Kunstler *et al.*, 2016). The other limitation of such approach is that it ignores the source of the variability. However, the validity assumption made on the higher level processes¹ may depends on the underlying mechanism. In *MountGrass* the explicit description of the intra-specific variability as a result of the phenotypic plasticity allows to avoid assumption and test directly the effect of this specific form of intra-specific variability. It appears that the phenotypic plasticity does not limits the coexistence by reinforcing the inter- versus intra-specific competition, but rather diminishes the competitive differences between species². This example highlight the strength of mechanistic approaches to investigate complex processes of which the underlying drivers may be ignored at the level of observation. The work of Zuppinger-Dingley *et al.* (2014) is another example on the complex links between intra-specific variability³ and coexistence mechanisms. They highlight the effect of the diversity of neighbours on the trait expression of species, showing potential positive feedback loops between functional and species diversity.

Other forms of intra-specific variability must be investigated, but it is likely that genetic variability results from fine scale selection processes (Hamann *et al.*, 2016), challenging the hypothesis of theoretical models. The intrinsic limitation of these approaches resides in the assumption that the source of the intra-specific variability (e.g. spatial or temporal heterogeneity leading to genetic variability or phenotypic plasticity) does not affect the common rule driving the interactions, while in many cases the interaction forces depend on the alteration of the conditions (see Choler *et al.* (2001) along elevational gradient) that also explains the intra-specific variability (see Kichenin *et al.* (2013) along similar gradient).

Mechanistic models should be used in complement of theoretical models. Theoretical models are easier to develop and test and may reveal interesting patterns. Mechanistic models can be used to investigated the underlying processes

THE SPECIFICITY OF THE MECHANISMS

¹ those that are impacted by the intra-specific variability, as opposed as those that cause this variability

² among other positive effects

³ here expressed by character displacement

of those patterns. But these models rely on strong empirical knowledge, patterns and data, that are costly to gather. This knowledge and data also nourish the development of new theories and theoretical models. This interdependency illustrates the need for collaboration between the different approaches in order to build and test theories that help us understanding the world around us.

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VI

SYNTHESIS & OUTLOOK

This short final chapter summarises the main results and advances produced during this PhD. It is also the opportunity to look ahead and trace future directions to extend upon this work. Imagining extensions to implement and questions to explore is an infinite game, and while many developments are proposed, I try to keep this discussion succinct and close to the current state of the model.

1 SYNTHESIS

1.1 A new agent-based model of mountain grasslands

The implementation of the model *MountGrass* was the opportunity to develop a new framework from scratch to tackle unresolved scientific questions. Thanks to the freedom that was given to me, I could approach the project in a personal way, establishing the foundation concepts, accumulating ideas, and developing a complex model of grassland communities.

The model developed had the ambition to fill the gap between fine-scale agent-based models, integrating physiological processes, fine-scale resource dynamics and phenotypic plasticity with large-scale community dynamics model, long-term dynamics of numerous species in a heterogeneous environment. Filling this gap is necessary to better understand and predict the dynamics of natural (and semi-natural) systems in the context of global change, affecting both climatic conditions and management scenarios. On one hand, computational cost and design choices limit our ability to deploy fine-scale models at large-scales to integrate the effects expressed at the local-scales. On the other hand, the large-scale community dynamic models overlooked some fine-scale processes such as intra-specific variability, and in particular phenotypic plasticity. Better integrating these two levels can help us better predict changes in the main properties of grassland communities, and the effect on ecosystem services.

FILLING THE GAP

MountGrass manages to fill this gap by integrating plant functioning and phenotypic plasticity into a framework based on the leaf economic spectrum and developed around strategic allocation trade-offs. The partitioned allocation to active and structural tissues regulates the balance between resource exchanges and respiration and tissue turn-over costs. These trade-offs enable a coherent representation of plant functioning while drawing a closed strategy space where the diversity of plant species can be modelled. This strategy space, which is at the core of the model, is also at the centre of the phenotypic plasticity conceptual framework developed in this work. The phenotypic axes drawn by the trade-off offers a space in which plant can evolve² based on their projection of external conditions. This projection is the engine that drives the phenotypic plasticity and allows the modelling of a strategic plasticity, that contrasts with ubiquitous plasticity. The implementation of multiple rules to drive this plasticity allows a comprehensive understanding of this mechanism of phenotypic plasticity and to test the robustness of the observed patterns.

² not in an evolutionary perspective.

While the steps of parametrisation highlight some progress to make in the implementation of phenotypic plasticity, the current version of *MountGrassoffers* stable growth patterns, both at the individual level and the community level, and a strong tool to start exploring effects of phenotypic plasticity. This stability is supported by the consistency of the results between the numerous parameter sets observed. Despite the difficulty to reproduce some specific empirical patterns, plasticity improves the performance of the model and impacts its behaviour, encouraging us to further explore its effects at the individual scale first, then at the community scale.

The strategy space built with independent strategy axes allows the modelling of a multitude of species. While the diversity offered by this new framework is not fully explored and used, the vegetative dimensions are extensively analysed. Because they are based on strong empirical trade-offs, these dimensions draw a wide performance landscape that (1) has the potential for high functional richness, and (2) evolves as a function of the resource levels. Establishing a link between this landscape with the plasticity mechanisms will be key to better represent phenotypic plasticity. This analysis also identifies the root mass fraction (RMF) dimension as a key trait to control plants performance, and therefore support the investigation of this axis as a plastic dimension.

CONSISTENCY

STRATEGIES AND PERFORMANCES

1.2 A better understanding of the effects of plasticity

The multiple plastic allocation algorithms, with varying plastic dimensions (RMF only, or in combination with the proportion of active tissues) and two alternative driving rules (maintenance of the equilibrium or growth optimisation), let us explore the potential effects of the plasticity. At the individual-scale the effects on growth and survival are analysed, and at the community-level the realised impacts on communities' properties are studied with plot simulations.

At the individual level, the main effects of plasticity are captured by the widening of the potential niche and the reduction of fitness differences. These modifications of the niche are explained by two main mechanisms: (1) the static gain in fixed conditions allows the convergence of plant individual phenotype to an optimum phenotype, this levels the competition but does not affect maximum growth. This convergence reveals a trade-off between species and functional diversities; (2) the dynamic gain, in variable conditions, enables the plastic plants to adapt their phenotypes over time, and increase the maximum growth rate relative to non plastic allocation maximum growth. This type of plasticity mostly favours exploitative species that would suffer more from resource variability under non plastic allocation. This effect could greatly affect predictions of the dominant species under climate change scenarios. While this gain also induces some convergence, and therefore a similar trade-off between species and functional diversity, it offers more potential for higher functional diversity, especially if plasticity has a physiological cost.

NICHES AND GAINS

The phenotypic plasticity can have contradictory effects on coexistence mechanisms, by the reduction of fitness differences on one hand and the reduction of niche differences, on the other hand. This paradox can be resolved by community-level simulation experiments. These experiments are also the opportunity to test the strength of the plasticity effects on productivity and community

identity.

A simple parameter filtering step ensures some stability of the community level simulations but does not offer enough information to disentangle the intricate effects of the multiple parameters.

The community-scale simulation experiments, over multiple seasons and sites, reveal a strong driving influence of daily weather on productivity. Despite a strong potential effect of plasticity on individual growth, the cumulative growth is not strongly improved under plastic allocation. These results suggest a limitation by carrying capacity, and an increase in the competition intensity to compensate for the reduction of abiotic filtering. Indeed, niche widening gives more species the opportunity to invade a habitat by reducing abiotic filtering. But the expected stronger biotic filtering effect of an increased competition is negated by the reduction of fitness differences between the coexisting species. The positive effect of plasticity is demonstrated by the invasion of species with higher plasticity ability.

This cumulative effect of the reduction of abiotic filtering and the reduction of fitness differences leads to changes in community and meta-community structure. Under plastic allocation, the abundance of the most dominant species is reduced, and numerous species are able to reproduce at low abundance. This shift in community structure, from a mono-specific or highly dominated community to a diverse community, goes with an increase in alpha diversity. But the larger number of species within one site also translates to a greater overlap in species distribution between sites. The sites show more distinct communities under non plastic allocation. The plasticity favours alpha diversity, while non plastic allocation better distinguishes the different sites because of more narrow and distinct niches.

The alteration of community and meta-community structures also affect the identity of the system and leads to less distinct community strategies and more variable identity over time. This effect can greatly affect overall dynamics under climate change, with progressive changes in the abundance and dominating strategy under plastic allocation, but rapid shifts in dominance under non plastic allocation, altering the meta-community dynamics.

The identification of clear mechanisms due to phenotypic plasticity that affects the community dynamics pushes to explore more in detail questions around these dynamics, especially in the context of climate change. Moreover, the framework developed based on the projection of external conditions and multiple allocation rules, does not completely solve the problem of the conceptualisation and implementation of the mechanism of the phenotypic plasticity. Further work needs to be done, but this model offers a promising basis and a reference point for future implementations. It also opens the door to approaches that link community dynamics with an epigenetic and genetic transmission of the information. These questions are further developed and discussed in the following section.

INTEGRATION AT HIGHER LEVEL

DIFFERENT DIVERSITIES & STRUCTURES

FURTHER EXPLORATION

2 OUTLOOK

This section explores further developments of the model. The first section focuses on how phenotypic plasticity is modelled, and how alternative approaches can help understand this process and its effects. The second part of this discussion describes ways to widen the scope of the model by taking advantage of already existing resources.

2.1 How to model phenotypic plasticity?

The framework developed during this project constitutes a step forward in the modelling of phenotypic plasticity. It integrates the idea of strategic plasticity (Bradshaw, 1965; DeWitt, 2016) within a phenotypic space drawn by allocation trade-offs that allows the modelling of diverse plant communities. However, the limitations shown by the current implementation reveal that the problem of phenotypic plasticity modelling is not resolved. While the question of plastic dimensions will always be present when modelling phenotypic plasticity, the main interrogations revolves around the drivers of the plasticity and the use of the information on environmental conditions available to individuals.

The idea of the plasticity as a strategy trait (Bradshaw, 1965; Bradshaw, 2006) was not fully explored despite being a centre point in the design of the model. This plasticity as a strategy, rather than a growing function, expresses the idea of limits that justify that not all species are plastic (Auld *et al.*, 2009; DeWitt *et al.*, 1998; Valladares, Gianoli, *et al.*, 2007; Van Kleunen & Fischer, 2005). These limits, in addition to be observed in natural systems, are also needed in the context of the model to avoid convergence and Darwinian demons. They are numerous and can be separated in multiple categories: actual limits that prevent an effective and reliable plasticity to increase the fitness, and costs that negate the fitness gain provided by the changes in phenotype. Valladares, Gianoli, *et al.*, 2007 also distinguish internal limits and ecological limits, but these are not always clearly circumscribed and quantified. The internal costs must be implemented in the model to avoid unnatural behaviours and explore emergent properties. The ecological limits, on the other hand should emerge from the mechanisms implemented. For example, the variability of the climatic conditions, should favour the selection of species with high plasticity in the current implementation of the model, if it is not too variable and unpredictable. This could be tested with simulations with two axes of treatment: temporal variability and auto-correlation. Mechanistic approaches, informed by the knowledge of plant biology, addresses the internal limits such as the morphological limits (Valladares, Gianoli, *et al.*, 2007), as implemented in Maire *et al.*, 2013 or Lohier,

EXPLORE THE LIMITS

2016, and to a lesser extend by the allocation trade-off in *MountGrass*. However, as observed in this implementation, the allocation trade-offs do not take into account the whole extent of the morphological limits, and further work is needed to quantify those. The mechanistic model also prevents unrealistic plasticity by the natural limitation of the phenotype flexibility (Forsman, 2014). The balance between the growth and the turn-over must be finely calibrated to capture this limitation of the plasticity that can cause lags in the plastic responses (DeWitt *et al.*, 1998). Other costs are harder to quantify, such as maintenance, acquisition and production costs. Methodologies are proposed to study the potential cost of plasticity (DeWitt *et al.*, 1998; Valladares, Sanchez-Gomez, *et al.*, 2006), but they have found limited effects in natural systems (Van Kleunen & Fischer, 2005), despite potential effects in a context of low genetic variation (Dechaine *et al.*, 2007). The difficulty of quantifying globally the plasticity costs comes from the difficulty to disentangle the different forms of cost (Murren *et al.*, 2015), the potential cost of homoeostasis (Kleunen & Fischer, 2007) and statistical limitations (Auld *et al.*, 2011). These difficulties are illustrated by the implementation of the cost of plasticity in *MountGrass*. The production cost, relative to the expression of an alternative phenotype different from the current phenotype, can intuitively be expressed as a function of the phenotypic distance between the two phenotypes (Valladares, Sanchez-Gomez, *et al.*, 2006). But the choices relative to the computation of this distance are numerous and hard to justify: should the current or the 'default' phenotype be the point of references, what axes are considered (composite traits such as the SLA, individual traits, morphological or chemical traits) and what are their relative importance, etc... The quantification of the costs of plasticity represents a challenge that requires progress and collaboration from the empirical studies, modelling approaches and statistical methods. This challenge is crucial for the quantitative estimation of the importance of plasticity in community dynamics.

As mentioned above, having a modelling approach closer to the molecular mechanisms would explicit some internal limits of the plasticity. In particular, the use of reaction norms would capture the complexity of the mechanism and the difficulty to integrate multiple signals. The prediction capacity would also be limited by the form of these reaction norms. The use of reaction norms also implies a high number of species specific parameters, increasing with the number of stresses considered. These arguments were invoked to justify the integrative approach of the model, but make the mechanism more grounded in reality.

The advantages provided by a molecular-inspired approach go beyond a better representation of the explicit limitations of phenotypic plasticity. Species specific reaction norms would at the same time allow more amplitude in the plasticity responses, but also more diversity (Kichenin *et al.*, 2013; Wellstein *et al.*, 2013). This method could easily model contrasted responses between avoidance and tolerance as a function of the global plant strategy (Pérez-Ramos *et al.*, 2013) or the available information (Heger, 2016). This diversity in responses also create the opportunity for phenotypic shifts outside the large scale trade-offs. Despite evidence of an economic spectrum at the intra-specific scale (Fajardo & Siefert, 2018; Hu *et al.*, 2015), the leaf economic spectrum does not totally control intra-specific variations (Fajardo & Siefert, 2018) and plastic responses are not driven by the same processes (Ryser & Eek, 2000). Molecular approaches should still be constrained by morphological and physiological limits, but not

A MOLECULAR-INSPIRED PLASTICITY

necessarily the same that determine the default plant strategies.

A molecular-inspired plasticity could better mimic the accumulation of stress molecules, leading to an increase in the amplitude of the plastic response following a second stress signal (Crisp *et al.*, 2016). This type of mechanisms also nicely illustrates the idea of species memory and the plant experience¹. The concept of stress levels, competing with the growth (Herms & Mattson, 1992) and eventually other forms of stress (frost, grazing, drought, etc...), was originally planned for the model, but the number of stresses were limited to avoid a too complex model. This limitation to resource-related stresses also led to the simplification of the plastic driving mechanism with the use of an integrative function². But this idea of competing stresses, based on molecular-inspired plasticity and plant-specific experience is attractive and should unlock a better understanding of the plasticity mechanisms under multiple stresses.

The framework developed during this work establishes plasticity as a strategy, but also includes the perception of external conditions as components of the overall strategy. These driving external conditions change within a season, justifying phenotypic plasticity, but also follow larger trends between seasons. These trends can lead to a gap between the default phenotype, or species memory of the external conditions³, and the average optimum phenotype, or average experience conditions. This gap can be detected by plants, even in the context of an adaptive phenotype. This is detected by the comparison of, depending on the context either (a) the experienced conditions, (b) the stress levels and (c) the direction of the plastic responses, with respectively (a) the species memory, (b) the absence of stress and (c) the average phenotype. The quantitative perception of this gap, expressed by directed plastic responses, can be transmitted to following generations in order to better fit to the general trend in the external drivers. This form of heritability can have a great effect on the community dynamics, particularly on their ability to cope with climate change. The heritability in intra-specific variable traits provides resilience to environmental disturbances and stabilises trait patterns (Barabás & D'Andrea, 2016).

The heritability of driven changes in phenotypes also makes sense in a molecular perspective. Indeed, a lot of plasticity mechanisms involve epigenetic inheritable mechanisms, such as histone modifications, DNA methylation or sequence modification (Nicotra, Atkin, *et al.*, 2010).

The heritability of driven changes in phenotypes, or driving traits such as the species memory, differ from random mutation and selection. However, the evolutionary process of mutation and selection of traits could lead to a greater understanding of the plasticity processes. First, it would allow the comparison between the dynamics of genetic and epigenetic modifications, and their relative impact on the community dynamics. If genetic modifications can lead to a community diversification, epigenetic modifications certainly increases the resilience to rapid environmental shift. Second, the incorporation of genetic algorithm would allow the selection of effective forms of plasticity, especially if the plastic responses are determined by reaction norms with species-specific parameters. The selection of the reaction norm forms, and the study of the species specific parameter distribution can greatly improve our understanding of this mechanisms.

The coexistence of epigenetic and genetic control can lead to particular phenotypic distribution. It may be important to consider such distributions to un-

¹ or *plant memory* as named in Crisp *et al.*, 2016, but *plant experience* is preferred here to avoid ambiguity with the concept of memory used in the model.

² function that consider all aspects of the plant growth by integrating all the processes for plant growth at the scale of the individual.

PLASTICITY, EPIGENETICS & GENETICS

³ as the two are linked in the model. Here I use these two terms to identify the species strategy expressed by the default phenotype, but depending on the species memory for the external conditions.

derstand plasticity strategies at the scale of the species (DeWitt, 2016).

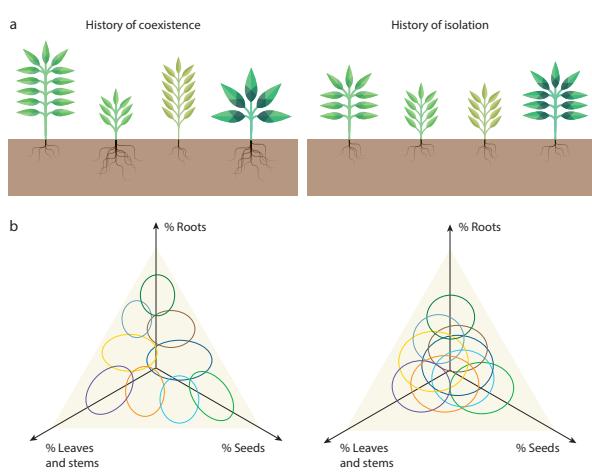


Figure 2.1: Evolutionary niche shifts. a) Zuppinger-Dingley *et al.*, 2014 find that, when plant species are grown in a common environment, those that have a history of selection in diverse communities develop greater differences in traits than species that have a history of isolation. b) This idea feeds into our understanding of how evolutionary history influences the ecological interactions of species that compete for growth factors such as soil nutrients, light and space. All species face trade-offs. For instance, biomass that is allocated to obtaining soil nutrients (roots) cannot be used to obtain light (leaves and stems) or to disperse to open sites (seeds). Graphically depicted, the resulting ‘trade-off surface’ (triangles) represents all possible ways in which plant species (ellipses) can allocate their biomass. A history of selection in diverse communities results in greater interspecific differences (less overlap of ellipses) and more specialization (smaller ellipses) than a history of isolation. From Tilman & Snell-Rood, 2014, reproduced with the permission of Springer, license number: 4386020602501.

The epigenetic changes, that link the experience of the external conditions with species strategies and transmits this information to following generations may play an important role in the character displacement observed in empirical experiments (Zuppinger-Dingley *et al.*, 2014). The ability of coexisting species to express contrasted phenotypes increasing the biodiversity may rely on the phenotypic plasticity (Roscher *et al.*, 2015), but epigenetic processes may play a role in the stability of this mechanisms and a long-time effect on biodiversity (see figure 2.1 and Tilman & Snell-Rood (2014)).

The development of implementations of the phenotypic plasticity as those listed above introduces a lot of complexity and computational costs. Another approach, at the conceptual end of the modelling approaches, is to consider the external resources and stresses as information to solve an investment problem. Once the gains and cost functions established, the reliability of the information, the uncertainty and the risks can be computed similarly as in other systems such as economic optimisation problems. This would extend the view of the plant physiology as an economic problem (McMurtrie & Dewar, 2011; Westoby *et al.*, 2000; Wright *et al.*, 2004). Such an approach relies on two sides: an explicit and precise description of cost and gain functions, and a prediction of the controlling variables. The former relies on a good understanding of plant physiology, and current knowledges allow a good representation of these processes, but the costs of the plasticity need to be better quantified as already highlighted. The reliability of the information for the prediction of the future conditions has already been pointed out in multiple studies (Auld *et al.*, 2009; DeWitt *et al.*, 1998; Richter *et al.*, 2012). The inability of a plant to consider the cost of being wrong is one argument explaining the low performances observed in *plastic-optimisation* simulations, despite a more flexible plastic allocation resulting in a better exploration of the phenotypic space. The productive, but less efficient phenotypes selected by this algorithm do not authorise errors in the prediction of the resource availability because of their higher sensitivity to unbalanced organ activities. The sensitivity could be considered by evaluating alternative projections of external conditions at the same time as the multiple phenotypes are evaluated. All alter-

IT IS ABOUT INFORMATION

native phenotypes would be evaluated for all probable future conditions. Then an averaging or ranking function would determine the target phenotype from the best phenotypes under the different projections. While it would increase the computational cost by increasing the dimension of the space explored, better implementation and exploration algorithms could compensate for this downside. In addition, the overall complexity of the model would almost stay the same as it would require only one additional model to weight the chance to optimise the fitness with the risk of unstable phenotypes in case of uncertain prediction.

More advanced learning processes can be investigated to model phenotypic plasticity. The concept of adaptive learning is also a path to explore for the development of the phenotypic plasticity. As genetic algorithms evaluate the success of a strategy by a fitness function at the end of a cycle, individuals could evaluate the performance of plastic response strategies after a few days. The driver of the plasticity resides in the evaluation of the current phenotype for the current and future conditions, in order to eventually develop alternative phenotypes if the performance is not satisfactory¹. Therefore, in the context of plastic phenotype, the evaluation step quantifies at the same time the success² of the current phenotype, but also the success of the plasticity that lead to this phenotype. The plastic strategy is evaluated through the improvement in the phenotype's success, rather than the absolute value of the fitness function. This relative change in fitness must also consider the external stress intensity to avoid penalising well performing plastic strategies under more intense stress. This evaluation of the plasticity strategy allows to adapt the parameters of the plastic response itself, but also the variables required to build the projection of condition, increasing the confidence and reducing the risks of the uncertainty mentioned above. This approach however makes sense under a complex and performing prediction algorithm, and may not fit the scope of the current model that focuses on community dynamics. Specific designs of plastic plant models will be required to explore this track.

2.2 Beyond the simple community

The previous part of the perspectives that can grow from this work focuses on alternative ways to model phenotypic plasticity or extend the current implementation. But the model already offers a novel tool to explore the effects of phenotypic plasticity on grassland communities dynamics. This aspect has only been scratched and more can easily be done with the current implementation.

The first look at the community results highlighted the importance of the fluctuations of the climatic variables. The work presented in the last part can be enriched by a finer analysis of the link between these variables and the properties of the communities. Two points in particular can be investigated: the response to the elevation gradient, and the stability of the productivity. The elevation gradient is of particular interest with the study system, as species response may be contrasted (Kichenin *et al.*, 2013), and plant interaction may evolve (Callaway *et al.*, 2002; Choler *et al.*, 2001) along this gradient. This last aspect could be investigated in the context of plastic allocation. Indeed, the plasticity may alter these interactions as the results at the community level suggest.

THE ROLE OF THE CLIMATE

¹ this sounds finalist, but I use this formulation to emphasise the phenotype evaluation step. This evaluation can take the form of a concentration in a certain stress molecule in a less perspective approach.

² any relevant fitness proxy.

This can be investigated with plot simulations or mixed-pot simulation to assess the direct interaction effects. While no clear productivity effect could be observed, the causes of this absence of change has to be identified. Changes in competitive interactions may hide potential effects of plasticity on productivity. In the context of climate change that will certainly increase the amplitude of climatic events (Gobiet *et al.*, 2014), the stability provided by plasticity in forest ecosystems (Morin, Fahse, *et al.*, 2014) should also be studied in mountain grasslands.

During this work, weather history as well as climatic projections have been gathered for multiple sites. This information can be used for the gradient analysis proposed above, but also the exploration of climatic scenarios. The combination of these scenarios (Intergovernmental Panel on Climate Change, 2014) with *MountGrassoffer* a powerful tool. Far from being realistic, the model still offers a way to model community dynamics with more temporal and spatial resolution and range than the transplant experiments deployed in empirical studies (Grassein *et al.*, 2014; Hamann *et al.*, 2016; Ishizuka & Goto, 2012; Wang *et al.*, 2014) to simulate the climate change alone, or in combination with management scenarios (Deléglise *et al.*, 2015). In particular it gives a way to model the dynamics of competitors (Alexander *et al.*, 2015) with linked communities, but also allows to simulate long-term dynamics and explore many scenarios at low costs.

The available data is not limited to weather data and community composition, as also site specific trait measures are available (from Chalmandrier (2015) and Deleglise (2011)). The combination of the site specific weather data with the community specific data should allow a stronger calibration of the global growth parameters. The difficulty to calibrate species specific parameters persists, but taking advantage of both local data, and world wide databases may solve this problem. In particular the estimation of some species specific morphological parameters should help define ranges for the proportion of active tissues, in agreement with composite traits such as SLA (John *et al.*, 2017) and SRL (Roumet *et al.*, 2016). While some of community level data is available for ungrazed plots, most of the mountain grasslands are exposed to natural and managed grazing. Similarly, frost constitutes a shaping factors of these communities that may be affected by climate change (Choler, 2015). Therefore, it should be accounted and modelled to fully capture the effect of external drivers shaping mountain grasslands. These two drivers, frost hazards and grazing or cutting events are both implemented but should be fully tested to gain realism in the modelled dynamics.

The suggested work on the calibration and testing of the management would allow a better quantification of the communities properties. In addition to allow the assessment of the ecosystem service for these sites (Bello *et al.*, 2010; Lavorel, Grigulis, *et al.*, 2011), the model could be used to test alternative management practices to optimize service levels (Goslee *et al.*, 2013). The grazing function is simple (pressure and selectivity parameters) but incorporate selective grazing linked to digestibility linked to the plant tissue density (Gardarin *et al.*, 2014). This functionality coupled with the fine description of the whole community is a handful tool to test scenarios and evaluate service trade-offs to select the best management pathway (Lafond *et al.*, 2015).

Considering multiple services is essential to select optimum management

CALIBRATION AND TESTING

ABOUT ECOSYSTEM SERVICES

practices to answer broad objectives. Because these service often rely on different properties of the ecosystem (Lamarque *et al.*, 2014; Lavorel & Grigulis, 2012) it is essential to better consider the potential synergies and feedback loops between these properties that were analysed in isolation during this project. Diversity-productivity relationship are often investigated (Lepik *et al.*, 2005; Tilman, Reich, *et al.*, 2001), but diversity-identity (Zuppinger-Dingley *et al.*, 2014) should also be investigated.

The benefit of having the weather data of multiple sites is also to be able to model explicit meta-community dynamics. While the communities composing the meta-community modelled in the previous were linked only by an infinite artificial seedbank, explicit links can be easily modelled. This seed-bank was necessary to establish the community and stabilise its dynamics. But, once the communities established, the invasion can be limited to the communities modelled rather than an the artificial seed-bank. This allows two things: first, the link between the communities can be explicit and parametrised (*e.g.* the volume of seeds exchanged between two communities can depend on the separating distance), secondly, meta-community-dynamics patterns can emerge from the specific community dynamics and these explicit links. This is interesting in the light of the results at the community levels that show a large impact of the plasticity on the community structure, increasing the species distribution overlap. Also, as mentioned, explicit meta-community dynamics can help us understand the migration/adaptation dynamics that can results from the climate change (Morin & Thuiller, 2009). Also, such link can help us model the different interactions that can arise from climate change, and how migrating species will compete with established adapting species (Alexander *et al.*, 2015). The plasticity certainly plays a particular role in these processes and may greatly alter the dynamics by promoting local adaptation (Frei, Ghazoul, Matter, *et al.*, 2014; Frei, Ghazoul & Pluess, 2014), especially if there is an asymmetry in the plastic capacity of the species as a function of there altitude of origin (Gugger *et al.*, 2015; Nicotra, Segal, *et al.*, 2015).

The long list of extensions to implement, calibrations to run and analysis to conduct that has just been discussed may contrast with the circumscribed perimeter of the work presented in this thesis. However, it shows that this model is a first step in the consideration of the sources of intra-specific variability, here namely the phenotypic plasticity, in the dynamics of the complex systems that are mountain grasslands. This work opens doors for further exploration, in addition to establish clear non trivial effects of plasticity on the properties and structure of the communities. While further work is needed to fully capture the complexity of plastic responses, it seems to me that the most interesting developments lie in the study of the effects of plasticity on larger-scale dynamics. Modelling these dynamics will be interesting to better identify the underlying processes, thanks to the mechanistic nature of the model, but also to predict future trajectories of these systems and optimise management scenarios.

THE META-COMMUNITY DYNAMICS

WRAP-UP

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LIST OF ACRONYMS

ABM: agent-based model

APR: adaptive plastic response

AU: arbitrary unit

BM: biomass

CWM: community weighted mean
(for traits)

DGVM: dynamic global vegetation
model

GPP: gross primary production

IBM: individual-based model (see
also ABM)

ISV: intra-specific variation

LDMC: leaf dry matter content

LDMC: leaf dry matter content

LES: leaf economic spectrum

LLS: leaf life-span

LNC: leaf nitrogen content

NPP: net primary production

ODD: overview, design concepts
and details

OM: organic matter

PAR: proportion of active tissue in
root

PAS: proportion of active tissue in
shoot

PFT: plant functional trait

RLS: root life-span

RMF: root mass fraction

RSR: root:shoot ratio

SDM: species distribution model

SLA: specific leaf area

SRL: specific root length

WUE: water use efficiency

ABSTRACT

Mountain grasslands provide numerous ecosystem services that are likely to be impacted by global change. Plant functional traits hold great promise to succinctly characterise plant community response to changing environmental conditions and its effect on associated services; with growing evidence of the importance of intra-specific trait variability. I propose here a novel agent-based model, *MountGrass*, that combines the modelling of species rich grassland communities with phenotypic plasticity. These two key components are integrated via allocation trade-offs based on established empirical patterns of strategic differentiation in resource-use.

With *MountGrass*, I explored the impact of phenotypic plasticity on individual plant growth and on main properties of grassland communities. At the individual level, the parametrised model revealed a strong impact of plasticity on growth and species' fundamental niches, with potentially large impacts on community properties. These effects are explained by the convergence of species' strategies and the reduction of the sensitivity to variable conditions. At the community level, simulations confirmed the strong effect of plastic allocation on community structure and species richness. These effects are driven by the cumulative effect of a reduction of both abiotic filtering and fitness differences between species. However, no clear effect on the dominant strategy or productivity could be detected.

Going further, the robustness of these findings and other patterns of community dynamics should be analysed with alternative or extended implementations of *MountGrass*. In sum, this work opens a door towards a better integration and understanding of the role of the intra-specific variability in complex plant community dynamics.

RÉSUMÉ

Les prairies de montagne offrent de nombreux services écosystémiques qui sont menacés par le changement global. Les traits fonctionnels constituent un outil prometteur pour caractériser les réponses des communautés à des changements de conditions environnementales et leurs répercussions sur les services associés. Cependant, des résultats de plus en plus nombreuses soulignent l'importance de la variabilité intra-spécifique des traits a également été mise en évidence. Pour étudier ces effets, je propose un nouveau modèle à base d'agents, *MountGrass*, qui combine la modélisation de communautés végétales riches en espèces avec des processus de plasticité phénotypique. Ces deux éléments au cœur du modèle sont associés grâce à des compromis d'allocation basés sur des patrons empiriques établis de stratégies d'utilisation des ressources.

Avec *MountGrass*, j'ai exploré l'impact de la plasticité phénotypique sur la croissance individuelle et les propriétés principales des communautés prairiales. À l'échelle individuelle, le modèle paramétré a révélé un fort impact positif de la plasticité phénotypique sur la croissance mais aussi sur la niche fondamentale des espèces. Des phénomènes de convergence et de réduction de la sensibilité aux variations de conditions expliquent ces effets. À l'échelle des communautés, les simulations ont confirmé de forts effets de la plasticité sur la structure des communautés et leur diversité spécifique. Ces effets sont expliqués par l'effet combiné de la réduction du filtre abiotique et de la réduction des différences de compétitivité. Cependant, aucun effet majeur sur la stratégie dominante ou la productivité n'a pu être mis en évidence.

Des implémentations alternatives ou des extensions du modèle devraient permettre de tester la robustesse des résultats obtenus et d'analyser d'autres schémas de dynamiques des communautés. En conclusion, ce travail ouvre la voie à une meilleure considération et une meilleure compréhension du rôle des variabilités intra-spécifiques dans les dynamiques des communautés végétales.