CLÉMENT VIGUIER

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

ABSTRACT

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

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

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

Aknowledgements

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

CONTENTS

I

INTRODUCTION

1 CONTEXT

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

1.1.1 The value of ecosystems: from properties to services

Everyone has a particular relationship with nature. The vision we put behind this word depends on the way we experienced nature, it can be temperate or tropical forest, mountain rivers or cliffs on the ocean littoral, bird songs or wind between stones. Anybody that shares one of these visions, I am sure wants to preserve natural systems. But facing this emotional perception and inner desire to see these ecosystems be preserved, other forces pushes in other directions. The reduction of biodiversity is increasing at dangerous rates, the deforestation threaten the largest forest systems, insects are less and less presents and animals are repelled to fragmented and diminishing habitats. Other logics than emotional attachment and will to protect impact all natural systems around the world. To be protected, the natural systems needed a way to be integrated in these logics, and the notion of ecosystem services was developed by **costanza_value_1997** This notion encompass all benefits human extract from ecosystems. It enables a categorisation of services and their quantification (that can go to the monetisation), and therefore allow them to be taken into consideration in global logic of capital, investment and value.

A NEW LOGIC

The notion of ecosystem services aims to capture the value of ecosystem, but what is this value?

SERVICES

If ones could be tempted to answer that the value of an ecosystem cannot be measures, it is clear that all ecosystems do not benefit to human in the same way. Face to the diversity of ecosystems and services they provide, we can try to develop a short answer for the object of study to this document: mountain grasslands.

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

Mountain grasslands provide numerous services, that can be divided in multiple categories such as provision, cultural and regulating services. 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 production for instance. Productivity is also interesting to assess carbon capture, a regulating service. Soil nutrient availability and water filtering are other regulating services impacted by the identity and diversity of species populating mountain grasslands. Finally, cultural services, related to tourism activity and landscape appeal are also related to grasslands species diversity.

In case of terrestrial ecosystems, vegetation cover is often central because of: it role of primary production, and the fact that vegetation community informs a lot on the properties of the abiotic and biotic conditions. Moreover, a most of studies on services from terrestrial ecosystem are interested in plants and soil invertebrate **de_bello_towards_2010** revealing the importance of vegetation in the provision of ecosystem services. In addition, in alpine habitats plant communities are susceptible to be the first impacted by 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.

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

PROPERTIES

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

- 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 diversity[2], 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 number of species or functional volume in the rest of this document.

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

Linking ecosystem services to ecosystem properties is essential both for the understanding of processes controlling these services, and for an easier quantification of such services. This is particularly important for the prediction of services levels to plan management practices in the context of global change. Some ecosystem services are here linked to the main community properties as illustrated in figure **??**.

[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

Mountain grasslands provide numerous ecosystem services

ecosystem services depends on abiotic, but also biotic factors and properties.

This structure is defined by the relative abundance of the different species of the community. Multiple drivers affect the relative abundance of a given species, from abiotic filtering processes to biotic interactions.

Need of mechanisms to produce dynamics and give properties.

The complexity of plant community dynamics requires mechanistic approaches to understand and predict system properties in new, extreme, and variable conditions.

The evaluation of ecosystem services relies on a precise description of the ecosystem abiotic and biotic properties. The plant community is the most dynamic and complex driver of ecosystem services, but direct links can be drawn between the fine description of the community and the ecosystem services. Understanding and prediction the main variables dynamics that capture those links is necessary to efficiently predict changes in ecosystem services levels. Plant communities are complex interconnected systems. In order to evaluate ecosystem services, they can be summarised by three main types of variables that capture different dimensions of such systems: the diversity, the productivity and the identity. These dimensions can be studied independently or jointly and give different information on secondary properties and provided services. But grassland communities are natural systems driven by environmental variables, and these drivers are changing leading to changes in services.

1.1.2 Global change: what changes and what consequences

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

Changes: Rising temperatures due to anthropogenic greenhouse gases has a strong effect on mountain climate.

Consequences: contrasting, depends on the factor: co2 or drought

trade-off lavorel and (**schirpke_multiple_2012**)

management change the position along these trade-off

climate also change things

1.2 Models: a solution to understand and predict complexity

1.2.1 The need for mechanistic models

outside what's known, extrapolations and experimentations

The combined effect of land-use mutations and climate changes will lead to environmental conditions never experienced by such systems. Predicting the

future in new conditions implies extrapolating multiple effects not tested in combination: with cumulative effects and potential synergies (carbon dioxide increase and grazing abandonment) or effects balancing each others (grazing abandonment and higher frequency drought events).

this title is not helpful -

combined effects

community responses: different processes (recruitment, growth, plasticity etc...) & levels (indiv, pop, metacommunity)

In addition to complexity of combined effects of global change drivers, complexity is inherited from the complexity of the community dynamics. Interacting species may change response of the system, and should be better taken into accounts (Gilman et al. 2010). To answer this challenge, large scale experiments are conduced such as Cedar Creek experiment in the United-States, or JENA experiment in Germany. These experiments give high value experimental data for various conditions and a variety of species, where interactions can be studied as well as management effects. Transplant experiments are also conduced to investigate the effects of temperature rise on the productivity, diversity and structure of the community. (Need more references) Showing increase in productivity and dicrease in diversity, as well as a shift toward more acquisitive species (**debouk_functional_2015**).

Observed effects: jung, transplant, effect on diversity and productivity.

contrasting effects as function of elevation: change in identity (abundance) and increased diversity in low altitude, but decrease in diversity in high altitude (Rosbakh, Bernhardt-Römermann, and Poschlod 2014)

But, temporal effects, history (that guy from ecoveg talk) hysteresis effect, metapop and invasion effects, balance between intra-specific and einter-sp responses...

Modelling approaches

limits of empirical studies: (Merilä and Hendry 2014)

(**schirpke_multiple_2012**)

The increasing variability in those conditions

and uncertainty that would require multiple experiments. Models allow to explore multiple scenarios.

1.2.2 The limit of classic patterns

niche vs process: stronger effects because no plasticity or local adaptation **morin_comparing_2009**

1.2.3 The rise of individual-based approaches

LINGRA-CC Rodriguez, Van Oijen, and Schapendonk 1999 to test gc effect on productivity : higher productivity allowing shorter intervals between cutting

Maire

Lohier: vegetative phase, coexistence and ontogeny...

Taubert: diversity productivity

1.2.4 When phenotypic plasticity makes things complicated

plasticity change response **morin_comparing_2009**

phenotypic changes in competition intensity that increase negative effect (Hänel and Tielbörger 2015)

plus ignored effects of intra-specific variations: additional level of response: amplification or mitigations, driver dependencies?

1.2.5 Gaps to fill

A wide range of models have been developed to better understand biological processes involved in plant growth and population dynamics, 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. It is not a problem in stable conditions, as the lower levels are implicitly integrated in the grain of larger processes (like the leaf gaz exchanges regulation processes are ignored at the scale of the population). But 2 things: (1) ok to not explicitly represent if know and considered within a broader mech (translated into assumptions: *e.g.*: assumption that stomata regulation), it is not the case of phenotypic plasticity as it is not considered in basic assumptions made. Plus, it depends on the scale, but daily growth require plasticity, period. (2) they may greatly change plant and community behaviour in changing conditon/environment.

scales and processes (climate, management etc...) put the resoure in the center (fate-hd)

process and mechanisms (Berger et al. 2008): effect on local env., adaptive beh, below-ground. partly filled (maire and Lohier).

but lack of species diversity and genericity.

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. But while action is needed, it requires understanding, and 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 intricate effects, mechanistic approaches should be priviledge.

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.

Ecosystem both living and non living components of a systems binded to-

gether by interactions.

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 these systems. However, they lack power to understand intricate systems and predict their dynamics, especially in case of uncertain scenarios.

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

In order to be compensate long development time and to extend the reach of experimental approaches, models should try to keep generic in structure and flexibility in use, while being specialised 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 plant functioning differences leading to diverse niches and possible response. 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 and community dynamics

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

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

2.3 Thesis overview

The rest of this thesis is divided in five chapters. The following chapter **??**, in the form of a literature review, introduces the concepts and knowledges 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 **??** and further extended. Chapters IV and V present respectively individual and community scale results of simulations made with

the developed model *MountGrass* on the effects of phenotypic plasticity on main plant community properties. Finally, the final chapter discusses the outcomes of this work and present path to follow from the present conclusions. Extensions to develop on the model are also proposed.

BIBLIOGRAPHY

Berger, Uta et al. (2008). "Competition among plants: Concepts, individual-based modelling approaches, and a proposal for a future research strategy". *Perspectives in Plant Ecology, Evolution and Systematics*. Space matters - Novel developments in plant ecology through spatial modelling 9.3–4, pp. 121–135.

Díaz, Sandra, Sandra Lavorel, Francesco de Bello, et al. (2007). "Incorporating plant functional diversity effects in ecosystem service assessments". en. *PNAS* 104.52, pp. 20684–20689.

Díaz, Sandra, Sandra Lavorel, Sue McINTYRE, et al. (2007). "Plant trait responses to grazing – a global synthesis". en. *Global Change Biology* 13.2, pp. 313–341.

Engler, Robin et al. (2011). "21st century climate change threatens mountain flora unequally across Europe". en. *Global Change Biology* 17.7, pp. 2330–2341.

Gilman, Sarah E. et al. (2010). "A framework for community interactions under climate change". *Trends in Ecology & Evolution* 25.6, pp. 325–331.

Hänel, Sabine and Katja Tielbörger (2015). "Phenotypic response of plants to simulated climate change in a long-term rain-manipulation experiment: a multi-species study". en. *Oecologia* 177.4, pp. 1015–1024.

Lavorel, S. and E. Garnier (2002). "Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail". en. *Functional Ecology* 16.5, pp. 545–556.

Merilä, Juha and Andrew P Hendry (2014). "Climate change, adaptation, and phenotypic plasticity: the problem and the evidence". *Evol Appl* 7.1, pp. 1–14.

Mountain Research Initiative EDW Working Group (2015). "Elevation-dependent warming in mountain regions of the world". en. *Nature Climate Change* 5.5, pp. 424–430.

Rodriguez, D., M. Van Oijen, and A. H. M. C. Schapendonk (1999). "LINGRA-CC: a sink–source model to simulate the impact of climate change and management on grassland productivity". en. *New Phytologist* 144.2, pp. 359–368.

Rosbakh, Sergey, Markus Bernhardt-Römermann, and Peter Poschlod (2014). "Elevation matters: contrasting effects of climate change on the vegetation development at different elevations in the Bavarian Alps". en. *Alp Botany* 124.2, pp. 143–154.

II

BACKGROUND: COMMUNITY DYNAMICS, TRAITS AND PHENOTYPIC PLASTICITY

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

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

1 UNDERSTANDING COMMUNITY DYNAMICS AND PROPERTIES: DRIVERS AND THEORIES

1.1 The different facets of plant communities: from processes to services

1.2 Community assembly and coexistence

Community assembly, drivers, interaction and dynamics.

1.2.1 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. Community were first viewed as group of species that have evolve together to survive within specific conditions. To maintain itself within the community, each species need to grow during the vegetative phase, survive, and reproduce. These steps of the life cycle result from the coordination of multiple physiological processes, supported by the extraction and use of essential resources: light, water and nutrients. A part of community ecology sees communities as discrete entities with specific characteristics. This view is particularly practical for management as the community type can be associated to 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 provide 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 consider that communities emerge from the distribution of individuals of a species, distribution controlled by its genetic and physiologic characteristics and its interactions with other species (gleason 1926, whittaker 1975). The distribution of individuals depends on how it is affected by abiotic conditions and interaction with other species, or biotic conditions. The joint

PLANT COMMUNITY

effects of abiotic and biotic environment are captured by the concept of niche (**elton_1927**). The niche of a species is defined by how a species population react to abiotic and biotic conditions (resource, competition, predation, survival) and how it impact its environment. Defining the niche of a species is primarily defining the barriers that constraint the distribution of the individuals of the species.

Based on genetic and physiological properties, plant species may be able to grow and reproduce in different climatic conditions.

ABIOTIC FILTERING

Potential niche

Abiotic filtering

Biotic filtering - realised niche.

BIOTIC FILTERING

Abiotic drivers main tnhing at global scale... Then interactions and competition.

The concept of ecological niche serves as a great tool for theoretical research on coexistence. It encompasses in a convenient way both abiotic and biotic filters of one species distribution. The Hutchitonian view of the niche also captures the multidimensionality of persistence and reproduction. However, niche concept does not make explicit the mechanisms that maintain coexistence.

1.2.2 The complexity of coexistence

If ones want to better understand and predict dynamics of complex systems, they first need to understand how such complex is assembled. If it is easy to observe diverse ecosystems (from bacteria, to plants, insects or algea), 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 image imagine biotic filtering as an physical filter, the same way abiotic filter is often illustrated, but this image does not translate the dynamic and complex nature of underlying processes. Biotic filtering emerge 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 to see the stability of the diversity.

THE QUESTION OF COEXISTENCE

Plankton paradox in homogeneous system, where abiotic and dispersion should have little role into maintenance of species diversity.

Focus on interaction: chesson modern coexistence theory.

Chesson vs Tilman. Chesson focuses on interaction and 2 by species, give central idea of stabilizing vs fitness difference.

Tilman focuses more on resources, how the use and impact on resources affect competition and can enable conexistence, but limited coexistence according to this criterion: plankton paradox. No heterogeneity, no temporal dynamics

Other things being equal hypothesis (in models at least) does not allow the full diversity to emerge.

(Clark et al. 2007)

Plant community require strong coexistence mechanisms to maintain species

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

1.3 Variability and dynamics: driven by the resource

1.3.1 Community dynamics

plant growth and life cycle

   Succession coexistence and forest models. Dynamics of resources, influx versus impact. Storage effects. Heterogeneity. But how does it link to traits.

   +

1.3.2 Heterogeneity: maintenance of diversity

tilman 1982, spatial chesson, 1994, temp, storage effect admer 2006 even if stochasticity can reduce coexistence. Fine scale heterogeneity is rarely taken into account, but can play an important role, especially with small individuals.

   Spatial and temporal heterogeneity play a major role in coexistence maintenance by creating various opportunity, or niches, in a given ecosystem. Other forms of temporal variations support stable coexistence.

   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 are not sufficient and driving processes must be considered. Explicit heterogeneity and dynamics of the resources is key to understand and model filtering processes, coexistence mechanisms and community dynamics. Modelling both community properties and resource dynamics require understanding of plant functioning and diverse growth strategies.

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 and niches. How such difference emerge from common functioning framework? Species differ on parameters that characterise this functioning. The challenge of modern community ecology is to determine the trajectories existing ecosystem will follow under new environmental conditions. Species centred approaches, because they are limited to the knowledge of existing response patterns to existing gradients, cannot tackle this problem. How can changes of the representation of plant allow generalisation of plant functioning to new condi-

tions?

2.1 The continuity of functional ecology

2.1.1 Shift in paradigm: traits and patterns

blabla bla

Measure of respiration, assimilation : better insight on the differences between species. Better understanding of plant functioning. Also show that there is a continum in plant functioning. This continuum is in line with the observed continum of community.

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

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 capture by abiotic variables, is primarily determined by the fitness components (and wheather 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 photsynthesis, water absorption, organic matter allocation, etc...) and the environmental conditions. Only considering these processes allow to explicit and decompose plant functioning, and therefore model it in new combinations of environmental conditions.

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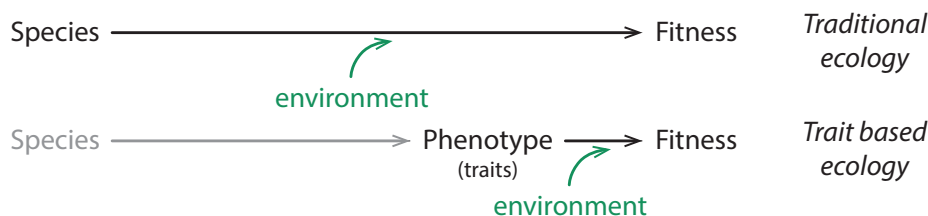
Figure 2.1: The shift toward trait based ecology allows for the decomposition of the link between species and fitness determined by the environment. On one hand, the link between species and traits is better characterised by standardised protocols and the use of databases such as TRY (**TRY**). On the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

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

phenotype of a species, ecologist can limit the representation effort to the link between traits and fitness physiological properties (P. B. Reich, Walters, and Ellsworth 1992), and then link species to traits with simpler data collection procedure (**cornelissen_handbook_2003**) (see figure 2.1, second row).

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

The functional traits allows to decompose the link between species and fitness, but requires an extra step as two links must be defined.

Collection of multiple trait sampling.

change of traits along gradients. Is it interesting?

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

2.1.2 Understanding interaction and competition: a question of symmetry?

Functional traits can be used to determine the response of species or communities to an abiotic factors, or link morphological traits to physiology. It is also argued that they can capture responses to biotic factors. Traits could be used to

CAUTION: do not mistake symmetry of competition (function of delta tratis) with form of competition (georges presentation).

niches and gradient - symetric vs hierarchical

symetric an assymetric interaction: it could change the interpretation: identify which traits are in what case.

(Kraft, Valencia, and Ackerly 2008) often need to use multiple traits (Kraft, Godoy, and Levine 2015)

traits used as a proxy for plant interaction and competition. /! can be context dependent (**gallaway_2003**).

but non transitivity: key role in maintenance diversity Levine et al. 2017.

Traits are good proxy for competitive interaction and fitness differences. .. a bit more complex. If the interaction is transitive, a strong asymmetric pattern can be observed between interaction effects and trait differences, while symmetric interaction reveal niche differentiation processes. Despite these observed relationship, alternative mechanistic solutions must be adopted to capture the multi-dimensional and context-dependent nature of plant interactions.

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

2.2 How trade-offs make strategy space

2.2.1 Trade-offs: capture constraints on species differences

The functional link that is observed between some morphological traits and physiological traits suggests underlying processes that link these traits together. It appears that multiple traits are correlated together at the global scale between species (P. B. Reich, I. J. Wright, et al. 2003; Ian J. Wright et al. 2004; Chave et al. 2009; Peter B. Reich 2014) and within species (Hu et al. 2015). This coorelation between functional traits of the leaf was described at a global scale by Ian J. Wright 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 ecologist to link quantitative measures to types of strategies that better capture diversity of strategies than discrete typology. These strategies are translated in traits, traits that can be translated into physiological processes parameters, then into components of fitness.

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

Similar correlations could be found in roots Ryser 1996; Peter B. Reich 2014

Where does it come from : shipley : morhpological constraints (as for seed size and seedling growth and survival), hard frontier plus soft frontier (small figure).

Diversity of mech: diveristy of strategies. more or less independent.

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. Better characterisation of these constraint should allow a better representation of plant functional diversity.

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 (- -).

2.2.2 Strategy-spaces made of trade-offs

Global functional trait dataset and databases revealed global scale correlations between traits. These correlations, or trade-offs, simplify the representation of plant species (Díaz et al. 2016) and translate fundamental axis of strategy differentiation (**reich_world-wilde_2013**). Yet, plant community 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

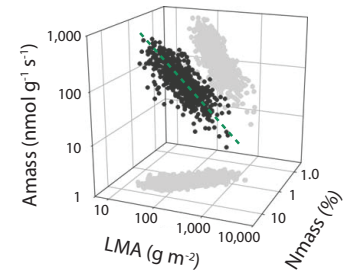(competitive pressure) constraints on combinations of functional traits. Therefore, for a given couple of traits, the physical independence of traits and the independence of ecological processes they are involved in should insure the absence of trade-offs between those. While some traits are related to multiple physiological processes (a composite traits like SLA is involved in water regulation, but also light capture), traits are often specific to a processes... Same number of strategy axis than filtering processes. (avoidance vs resistance, drough, frost, but could be applied to competition for resources)

reich, wright, shipley, diaz.

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

2.3 How traits link to ecosystem properties

The link between community properties and ecosystem services has been mentioned in chapter I, this section develops processes involved and how functional traits are integrated into this link.

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

As explained, plant species, based on their identity, provide ecosystem services. Some of these services are direct consequences of the characteristic of the species and their functioning. The greater the abundance of a species that supply particular ...

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

grime1998, shipley 2006 **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 wide audience. This measure is peculiar to groups of organisms and plays a major role in its functioning and the services it provides. Diversity can refer to species richness or functional diversity. The former quantifies the number of species present in a habitat and can take into account the relative abundance of the species. Many indexes can be used to measure this variable representing different perspective or aspect of the metrics (see Chalmandrier 2015 for exhaustive information).

Empirical studies demonstrate the importance of diversity for multi-dimensional services ... Services are: ......

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

First importance of species richness in found in the insurance effect that prevent the loss of a function or a service with the loss of a species by insuring that multiple species provide such function or service. 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, as each species added can provide new function/service (or at worst reinforce already present ones). This second concept is at the edge of the insurance effect

benefit of species diversity: insurance effect - portfolio effect ?

selection, niche complementarity

what about functional convergence

productivity
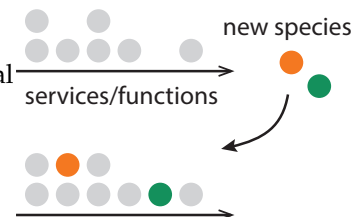
Figure 2.3: Insurance and selection effects. New species increasing diversity either reinforce existing function (•), or provide new function (•)

2.3.3 Productivity: both community property and ecosystem services

Productivity of a plant community is mostly sensitive to abiotic conditions (precipitation and temperature). Productivity as a marker of abiotic conditions and

Productivity as a property: depends on the community structure and properties. Leads different services.

Productivity as a service itself: production (fodder in this case, but OM in forests).

2.3.4 Trade-offs in ecosystem properties

lavorel 2012 : trade-off (Sandra Lavorel and Grigulis 2012) traits - related to trade-off in ES bundles, mostly driven by climate change (rather than management) (Lamarque et al. 2014) limits ?

The shift from species centred paradigm to trait approaches unlocked numerous discoveries in plant community ecology. In addition to facilitate the study of the effect of abiotic conditions and biotic interaction, traits can be used to describe the community and its main properties to evaluate ecosystem services.

2.4 Modelling diverse plant community

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

2.4.1 How strategy space open vegetation modelling

Plant diversity is expressed and in visible to anyone by the variation in shapes and colors, scents and growth forms, but this diversity is the demonstration of the multiplicity of strategies. In a early attempt to make sense of this diversity of strategy Grime 1977 theorise the existence of two type of constraints that shape plant communities: perturbations and stress. The perturbation axis captures the variability of community drivers, while the stress axis captures how conditions facilitate or make difficult plant establishment. They draw a two-dimensional space where three regions can be invaded[1], 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* fgure 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 specificaly captured by such wide concepts. Westoby 1998 highlight the difficulty to use such space and its incapacity to explain some patterns. According to him, a strategy space[1] should:

- "express meaningful differences in ecological behaviour between species";

- allows to "position a plant species from anywhere in the world within";

- be composed of attributes that "require little enough effort to estimate";

- lets "possible to quantify the extent to which the [strategy-space] captures variation in other plant attributes".

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

- Specific Leaf Area (denoted L): captures the speed of return of investment of carbon in leaf, as latter highlighted in the LES. High SLA is generally associated to competitive species that capture a lot of light and have a high growth rate. At the other end of the spectrum, low SLA species are more stress tolerant. This axis is the practical equivalent to hte axis CS in GRime's triangle.

THEORY TO TRAITS

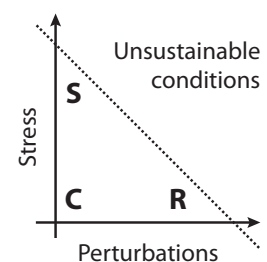[1] high stress and high perturbation regions does not allow establishment

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

[1] called Plant Ecology Strategy Scheme (PESS) in his paper

- Height at maturity(H): race to the light (but not time fixed as protocol for functional trait encouraged it), but also capture ruderal axis (time interval between perturbations)

- Seed mass (S): expresses the capacity of a species to invade freshly disturbed environments or the competitive advantage seedlings possess with a larger starting carbon pool. This trade-off between competitive strength of seedlings against 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

Strategy space proposed by Westoby   IN DGVMs

Dynamics Global Vegetation Models tend to use such strategy spaces to model high diversity with limited number of traits.

Simplification: limited number of straits: DVGMs

translate traits into physiology: easy

diversity of strategies

specific trade-off related to the context (Scheiter and Higgins 2009)

why not too much on IBMs (but Reineking, Marechaud ?, falster, meh, I guess   IN IBMs
that Lohier's and Maire's are sort of strategy space) - because lower community models at this scale: gap to fill.

But when it's used: break the growing function that links phenotype, genotype and environment (see figure 2.1). Same growing function: no need for specific parameters: smae rules for all, but different phenotypes. (the concept of genotype and phenoptype would merge for functional traits, if there was not other control on other aspects, phenotype defines itself). This is important as it allows for intra-specific variations that would necessite more complex function in the first paradigm.

The growing function, in a simulation model includes all steps from resource gathering and transformation, biomass allocation and phenotype alteration (*e.g.* frost, graing *etc*...), takes as inputs the phenotype and environment, and gives the new state of the phenotype (and environment).

figure 2.1

This last paragraph is important to link with the plasticity in a later paragraph.

2.4.2 How models inform us on properties and dynamics

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

and ignore the individual variations.

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

3.1 Intra-specific variability change the rules

3.1.1 Increasing interest in intra-specific variations

Trait approaches emergences 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 extend of the intra-specific variation is a big question as some ecologists point out because trait based approaches make sense only if inter-specific differences are greater than intra-specific differences. While this can be discussed, high functional variability within the species would weaken theories and generalisation based of mean traits. Violle et al. 2012 suggest that the extend of within population variability relatively to within community variability should be considered and avoid mistakes in the estimation of coexistence mechanisms. Ignoring intra-specific variability lead to underestimation of niche overlapping, plastic response to neighbours or the fraction of resource a species can used. Multiple studies focused on the extend of functional intra-specific variability (Cécile Hélène Albert, Thuiller, Yoccoz, Soudant, et al. 2010; Cécile Hélène Albert, Thuiller, Yoccoz, Douzet, et al. 2010) and how to disentangle this vairability from species turn-over (Lepš et al. 2011) in community response. These studies show contrasting results between traits and levels. Cécile Hélène Albert, Thuiller, Yoccoz, Douzet, et al. 2010 demonstrate a within species variability explaining between 20% and 40% of total trait variance, and Siefert et al. 2015 note similar levels, but this fraction tends to decrease with the increasing community diversity. They also show that the strategic differentiation between exploitative and conservative species is robust to these variations. It appears that all traits are not variable to the same degree and traits like SLA, height, LNC and LDMC are relatively variable while leaf morphology traits variability is lowerSiefert et al. 2015.

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

The relative extend of intra-specific variability depends on the trait, spatial

EXTEND

extend and species richness, but not on climatic conditions (Siefert et al. 2015) suggesting general mechanisms

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

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

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

After the emergence of trait-based ecology and its high potential, recent focus on intra-specific trait variability question the strength of such approaches. While intra-specific variability does not negate numerous conclusions from previous work, because of its large extend and how it alters functional diversity, its effects on community dynamic processes must be interrogated, and underlying mechanisms investigated.

3.1.2 Contrasting effects of intra-specific variations

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

Jensen inequality ... Intra-specific variability can affect
    Hart: why it is not enough

ISV also effect of abiotic filtering
    affect on realised niche
    neighbours: avoid or increase competition

specifically on diversity
    callaway 2003 from competition to facilitation.
    Bolnick et al. 2011 (Hart, Schreiber, and Levine 2016) (Courbaud, Vieilledent,

and Kunstler 2010) (Turcotte and Levine 2016) (Roscher et al. 2015) (Valladares et al. 2015) (**barabas_effect_2016**) (Jung, Violle, et al. 2010)

The intra-specific variability has been observed to be an important part of community functional diversity, but also a way the community respond 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 their understand potential effect on ecosystem dynamics.

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

There is a difference between how we obsere ISV, and why it emerges. What is random? Therefore it is ... not good ... to apply such simplification of random effect onto theoretical models to predict the effect of intraspecific variability with strong assumption (observed on functional trait in wide spatial range, applied to interactions in homogeneous context) on how they translate onto interactions (done in Halt, check Boltnick) Cécile Hélène Albert, Thuiller, Yoccoz, Soudant, et al. 2010 bell shape intra-specific response pattern along gradient, but doesn't stand according to Kichenin et al. 2013. Depends on trait and gradient... cannot assume that, need real quantification. ok if not a gradient response (or gradient is not known). Bell shape can emerge from non measure gradient with linear response.

Dewitt and Barabas.

The same way the neutral theory is simplifying and brings little understanding to underlying processes and relies on strong hypothesis, considering intra-specificity as a purely random mechanism is insufficient.
Bell shape do not appear in altitude gradient... inconsistencies between theory and empirical data
Strong theoretical hypothesis
refer to asymmetric and symmetric competition

If most of changes are plasticity or selection: it changes the effects on interactions and niche.
What are the possible effects? probably it does not affect interaction like (Hart, Schreiber, and Levine 2016) supposes (even if they talk about variations, their conclusions may not be extendable to plastic variations). May change a lot the balance between abiotic filtering and biotic filtering.
– go to indivdual mechanisms, evolution could tackle genetic variations, physiology and ecology on ontogeny, and evolution and ecology on phenotypic plasticity

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

Ecology shifted from species to traits syndromes with great success, but

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

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

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

3.2.1 The different sources of intra-specific variability

Intra-specific variation can be caused by to two mechanisms: genetic variation and phenotypic plasticity. Genetic variation occurs when individuals from the same species have different genotypes, leading to different phneotype. On the other hand, phenotypic plasticity implies that a same genotype can lead to different phenotypes. Plasticity may involve epigenetic mechanisms (Adrienne B. Nicotra et al. 2015) that blur the frontier between the two forms of intra-specific variability as epigenetic is a inheritable form of plasticity. It is transmitted to descendants but unlike genetic mutation is reversible. To keep thing simple, epigenetic phenomenons 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 explain by the treatment, it is a plastic response Frei, Ghazoul, and Pluess 2014, and a large fraction of the variability observed in grasslands species is plastic response rather than genetic variation alone Frei, Ghazoul, and Pluess 2014; Merilä and Hendry 2014.

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

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

3.2.2 What is phenotypic plasticity?

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

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.
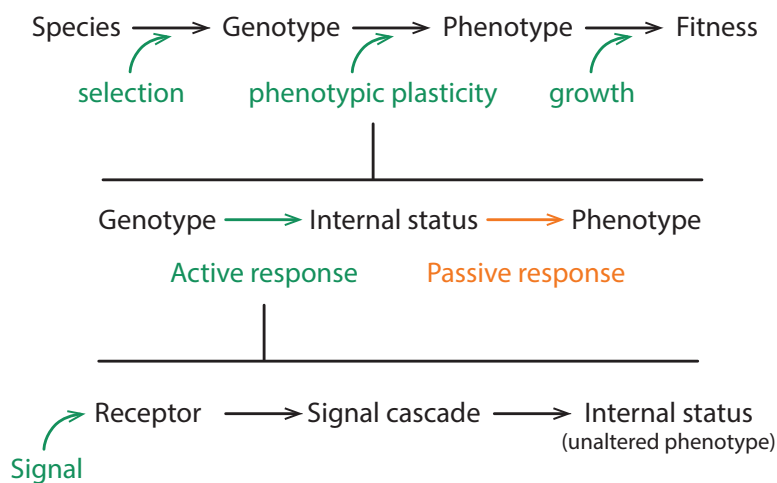
Figure 3.1: Decomposition of phenotypic plasticity as a step between the genotype and the fitness. Phenotypic plasticity is the effect of environment on the link between genotype and phenotype. Plasticity can itself be decomposed in active plastic response that change the internal status of the individual (under genetic control) and passive response that result from inevitable effect of environment of the traits on the individual.

Active and passive plastic response can be discriminated by the position of the control: internal for active plasticity, or external for 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 3.1) as summarised in figure 3.2.

Changes in phenotypes are controlled mainly by changes complex development processes. These processes involve numerous proetins 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 **??** in relationship

with gene expression pathway (see also A. B. Nicotra et al. 2010).

Active phenotypic plasticity is an integrative process at the scale of the individual that aims for an improvement of plant fitness by the adjustment of its morphology according to environmental cues. It often relies on multiple regulation processes. Modelling the extend 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

Plastic response can involve numerous genes interaction in networks of regulation pathways. The objective of an ecological model is not to reproduce this complexity, but the basic behaviours emerging from this biological complexity[1]. 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 predict different phenotypes for plants sharing the same phenotype (often just defined by the species affiliation) growing in different condition. But most of this plasticity is passive, and it could be encompassed in this personnal definition of the notion of growing function (see figure **??**). However, among vegetation models only some of them claim to include phenotypic plasticity (Maire et al. 2013), why so? What criterion can be used to distinguish active from passive plasticity in the context of plant modelling?

The use of information from environment to change the phenotype in order to have a better fitness is active plasticity. But in practice[1], nothing really separates the two as local environmental variables are used to determine the phenotype of a plant in both cases. However, the justifications and the forms of the linking functions are different, and they may involve different traits. This idea is illustrated in figure **??**, where the phenotype is defined by[2] then controlled by the growing function as a function of current phenotype and environment. In the paper of Maire et al. 2013, as it is often the case, plasticity is just an additional form of growing function. There is not differences between plasticity of two species, if two species have the same phenotype, then in similar environment they would express the same plastic response. I argue that plasticity, to be considered as an active process, should be under a genetic control (*i.e.* species specific parameter). This mean that, despite a shared rule, and similar phenotype, the plastic would be different and would depend on a species specific parameter.

Two questions emerge from this: if growting function and plastic response are different (conceptually), how to build each of these functions? How the genetic control affect the

However, the linking function used have different justifications and forms, and act of potentially different traits. In order to mimic active plasticity observed in nature the environmental variables should be integrated by plants, however this integration function is often ignored Maire et al. 2013. Therefore plasticity is mostly framed by the traits that are affected by the

every model plastic, but mostly passive

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

Physical signal

Integration
(receptor)

Transmission
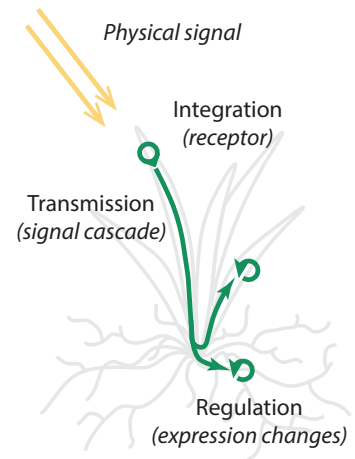*(signal cascade)*

Regulation
(expression changes)

Figure 3.2: 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 limited number of basis biological units living organism are made of, and the emergence throuth simple mutation-selection operation. This complexity can be mimic by simpler and freer mathematical design.

REFERENCE AND PLASTIC TRAITS
[1] in models

[2] or merged with, see figure **??**

acterise the response.

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

resources, but also risk (frost, grazing): alter cost and gains.

not often prediction, but just reaction norms: in that sense it is close to nature functioning, but ignore evolutionary mechanisms that selected these reaction norms (can take an more deterministic perspective on the matter).

Or perfect optimisation with perfect estimation of condition.

3.3 Toward an integrative framework of plant strategy and phenotypic plasticity

3.3.1 Flexible strategies

3.3.2 Plasticity as a strategy

Bradshaw? Dewitt

frame of reference: does not allow the interrogation of plasticity as a strategy. All plant share the same plasticity.

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 an 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 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 phenomena and the consequences for plant communities.

3.4 How phenotypic plasticity affect ecosystem properties and dynamics

reduce invasion and extinction because no local adaptation or pl **morin_comparing_2009**

3.4.1 Contrasting effect on diversity

Convergence ?

biche filling versus competitive exclusion: assymetric gain and coexistence theory.

3.4.2 Productivity always improved?

Species able to deal with variations: stay relatively (mor ethan withou PP) when conditions doesn't match.

pinus sylvestris gretter pl better in variable environment Richter et al. 2012

Maintain different species: may change the productivity pattern. better at low prod, lower prod by introducing less productive species.

3.4.3 Community identity shift

3.4.4 Phenotypic plasticity effect on individuals and communities

Why we need this model:

BIBLIOGRAPHY

Albert, Cécile Hélène, Wilfried Thuiller, Nigel Gilles Yoccoz, Rolland Douzet, et al. (2010). "A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits". en. *Functional Ecology* 24.6, pp. 1192–1201.

Albert, Cécile Hélène, Wilfried Thuiller, Nigel Gilles Yoccoz, Alex Soudant, et al. (2010). "Intraspecific functional variability: extent, structure and sources of variation". en. *Journal of Ecology* 98.3, pp. 604–613.

Albert, Cécile H. et al. (2012). "On the importance of intraspecific variability for the quantification of functional diversity". en. *Oikos* 121.1, pp. 116–126.

Bello, Francesco de et al. (2011). "Quantifying the relevance of intraspecific trait variability for functional diversity". en. *Methods in Ecology and Evolution* 2.2, pp. 163–174.

Bolnick, Daniel I. et al. (2011). "Why intraspecific trait variation matters in community ecology". *Trends in Ecology & Evolution* 26.4, pp. 183–192.

Chalmandrier, Loïc (2015). "From communities to meta-communities : decrypting diversity patterns". PhD thesis.

Chave, Jerome et al. (2009). "Towards a worldwide wood economics spectrum". en. *Ecology Letters* 12.4, pp. 351–366.

Clark, James S. et al. (2007). "Resolving the biodiversity paradox". *Ecology Letters* 10.8, pp. 647–659.

Courbaud, Benoît, Ghislain Vieilledent, and Georges Kunstler (2010). "Intra-specific variability and the competition–colonisation trade-off: coexistence, abundance and stability patterns".

Díaz, Sandra et al. (2016). "The global spectrum of plant form and function". en. *Nature* 529.7585, pp. 167–171.

Diaz, S. et al. (2004). "The plant traits that drive ecosystems: Evidence from three continents". en. *Journal of Vegetation Science* 15.3, pp. 295–304.

Frei, Esther R., Jaboury Ghazoul, and Andrea R. Pluess (2014). "Plastic Responses to Elevated Temperature in Low and High Elevation Populations of Three Grassland Species". *PLOS ONE* 9.6, e98677.

Grime, J. P. (1977). "Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory". *The American Naturalist* 111.982, pp. 1169–1194.

Hart, Simon P., Sebastian J. Schreiber, and Jonathan M. Levine (2016). "How variation between individuals affects species coexistence". en. *Ecol Lett* 19.8, pp. 825–838.

Hu, Yu-Kun et al. (2015). "Novel evidence for within-species leaf economics spectrum at multiple spatial scales". *Front. Plant Sci.* P. 901.

Jung, Vincent, Cécile H. Albert, et al. (2014). "Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events". en. *J Ecol* 102.1, pp. 45–53.

Jung, Vincent, Cyrille Violle, et al. (2010). "Intraspecific variability and trait-based community assembly". en. *Journal of Ecology* 98.5, pp. 1134–1140.

Kichenin, Emilie et al. (2013). "Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient". en. *Funct Ecol* 27.5, pp. 1254–1261.

Kraft, Nathan J. B., Oscar Godoy, and Jonathan M. Levine (2015). "Plant functional traits and the multidimensional nature of species coexistence". en. *PNAS* 112.3, pp. 797–802.

Kraft, Nathan J. B., Renato Valencia, and David D. Ackerly (2008). "Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest". *Science*. New Series 322.5901, pp. 580–582.

Lamarque, Pénélope et al. (2014). "Plant trait-based models identify direct and indirect effects of climate change on bundles of grassland ecosystem services". en. *PNAS* 111.38, pp. 13751–13756.

Lavorel, S. and E. Garnier (2002). "Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail". en. *Functional Ecology* 16.5, pp. 545–556.

Lavorel, Sandra and Karl Grigulis (2012). "How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services". en. *Journal of Ecology* 100.1, pp. 128–140.

Lepš, Jan et al. (2011). "Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects". en. *Ecography* 34.5, pp. 856–863.

Levine, Jonathan M. et al. (2017). "Beyond pairwise mechanisms of species coexistence in complex communities". en. *Nature* 546.7656, pp. 56–64.

Maire, Vincent et al. (2013). "Plasticity of plant form and function sustains productivity and dominance along environment and competition gradients. A modeling experiment with Gemini". *Ecological Modelling* 254, pp. 80–91.

Merilä, Juha and Andrew P Hendry (2014). "Climate change, adaptation, and phenotypic plasticity: the problem and the evidence". *Evol Appl* 7.1, pp. 1–14.

Nicotra, A. B. et al. (2010). "Plant phenotypic plasticity in a changing climate". *Trends in Plant Science* 15.12, pp. 684–692.

Nicotra, Adrienne B. et al. (2015). "Adaptive plasticity and epigenetic variation in response to warming in an Alpine plant". en. *Ecol Evol* 5.3, pp. 634–647.

Niinemets, Ülo (2001). "Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs". *Ecology* 82.2, pp. 453–469.

Poorter, Hendrik, Ülo Niinemets, et al. (2009). "Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis". en. *New Phytologist* 182.3, pp. 565–588.

Poorter, Hendrik, Karl J. Niklas, et al. (2012). "Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control". en. *New Phytologist* 193.1, pp. 30–50.

Reich, P. B., M. B. Walters, and D. S. Ellsworth (1992). "Leaf Life-Span in Relation to Leaf, Plant, and Stand Characteristics among Diverse Ecosystems". *Ecological Monographs* 62.3, pp. 365–392.

Reich, P. B., I. J. Wright, et al. (2003). "The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies". *International Journal of Plant Sciences* 164.S3, S143–S164.

Reich, Peter B. (2014). "The world-wide 'fast–slow' plant economics spectrum: a traits manifesto". en. *J Ecol* 102.2, pp. 275–301.

Richter, Sarah et al. (2012). "Phenotypic plasticity facilitates resistance to climate change in a highly variable environment". en. *Oecologia* 169.1, pp. 269–279.

Roscher, Christiane et al. (2015). "Contrasting Effects of Intraspecific Trait Variation on Trait-Based Niches and Performance of Legumes in Plant Mixtures". *PLoS ONE* 10.3, e0119786.

Ryser, P. (1996). "The Importance of Tissue Density for Growth and Life Span of Leaves and Roots: A Comparison of Five Ecologically Contrasting Grasses". *Functional Ecology* 10.6, pp. 717–723.

Scheiter, Simon and Steven I. Higgins (2009). "Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach". en. *Global Change Biology* 15.9, pp. 2224–2246.

Siefert, Andrew et al. (2015). "A global meta-analysis of the relative extent of intraspecific trait variation in plant communities". en. *Ecol Lett* 18.12, pp. 1406–1419.

Turcotte, Martin M. and Jonathan M. Levine (2016). "Phenotypic Plasticity and Species Coexistence". *Trends in Ecology & Evolution* 31.10, pp. 803–813.

Valladares, Fernando et al. (2015). "Species coexistence in a changing world". English. *Front. Plant Sci.* 6.

Violle, Cyrille et al. (2012). "The return of the variance: intraspecific variability in community ecology". *Trends in Ecology & Evolution* 27.4, pp. 244–252.

Westoby, Mark (1998). "A leaf-height-seed (LHS) plant ecology strategy scheme". en. *Plant and Soil* 199.2, pp. 213–227.

Wright, Ian J. et al. (2004). "The worldwide leaf economics spectrum". en. *Nature* 428.6985, pp. 821–827.

III

Modelling alpine grasslands with MountGrass, a generic framework integrating phenotypic plasticity

IV

INDIVIDUAL PERFORMANCE: STRATEGY AND PLASTICITY

V
COMMUNITY DYNAMICS

VI

SYNTHESIS & OUTLOOK

GLOSSARY

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

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

Plasticity

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