

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.

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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

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.

NEW LOGIC

But, what is the value of an ecosystem?

SERVICES

If ones could be tempted to answer that the value of an ecosystem cannot be measure, it is are to deny 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.

The ecosystem services are tightly related to ecosystem properties (as illustrated in figures ??), that can be extracted from the description of the grassland communities. But grasslands community are natural systems driven by environmental variables, and these drivers are changing.

### 1.1.2 Global change

Mountain grasslands are maintained by strong climatic constraints that limit growth rate and lifeforms (**koerner\_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 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, stronger isolation (island effect due to rise in temperature) and reduction of the grazing pressure.

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

CLIMATE CHANGE

trade-off lavorel and (**schirpke\_multiple\_2012**)

management change the position along these trade-off  
climate also change things

EFFECT OF MANAGEMENT

### 1.1.3 The need for mechanistic models

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).

A NEW WORLD

this title is not helpful -

COMPLEXITY

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 conducted such as Cedar Creek experiment in the United-States, or JENA experiment in Germany. These experiments give high value experimental data for various conditions and a variety of species, where interactions can be studied as well as management effects. Transplant experiments are also conducted to investigate the effects of temperature rise on the productivity, diversity and structure of the community. (Need more references) Showing increase in productivity and decrease 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 inter-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 Community dynamics: complexity emerging from parts and the role of phenotypic plasticity

title too vague to bring meaning, should put both parts together.

### 1.2.1 The limit of classic patterns

niche vs process: stronger effects because no plasticity or local adaptation morin\_comparing\_2009

### 1.2.2 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

### 1.2.3 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)

### 1.2.4 Gaps to fill

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

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

lack of diversity.

## 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 privileged.

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

**Ecosystem** both living and non living components of a systems binded together 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-specific variations are especic 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.

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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

### 1.1.1 From community description to ecosystem services: the facets of the community

Ecosystem services are various. Some of them can be easily assess (e.g. fodder production and quality), while others are more subjective (cultural or recreational services) or hard to measure (carbon sequestration, water purification etc...). But all of them rely on a good description of the system, even though this description do not have to be complete as certain aspect of an ecosystem might not be relevant to all provided services. 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.

In case of terrestrial ecosystems, vegetation cover is often central because of: its 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** 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. These reasons support the central role of vegetation in ecosystem services assessments. The question of the description and prediction of plant communities properties and dynamics will be addressed more in details in the following sections of this chapter, but it is important to establish the main components of a vegetation community link with provided services.

The loss of species can impact services in two different ways: first losing species may lead to the reduction, or disappearance, of a service associated to a particular species; second, some services are directly related to the species diversity itself.

DIVERSITY  
IDENTITY  
PRODUCTIVITY

Mountain grasslands provide numerous ecosystem services

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

**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.**

### 1.1.2 From processes to properties

The assessment of ecosystem services relies on a detailed characterisation of the community structure and properties. The knowledge of species characteristics and relative abundance allows the computation of summary variables that characterise the plant community. Long history of plant study and description gives us good knowledge of benefit provided by specific species. <sup>2</sup> 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.

## 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

PLANT COMMUNITY

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 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 coexistence, 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 conditions?

## 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 continuum in plant functioning. This continuum is in line with the observed continuum 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.

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 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 photosynthesis, water absorption, organic matter allocation, etc...) and the environmental conditions. Only considering these processes allow to explicit and decompose plant functioning, and therefore model it in new combinations of environmental conditions.

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

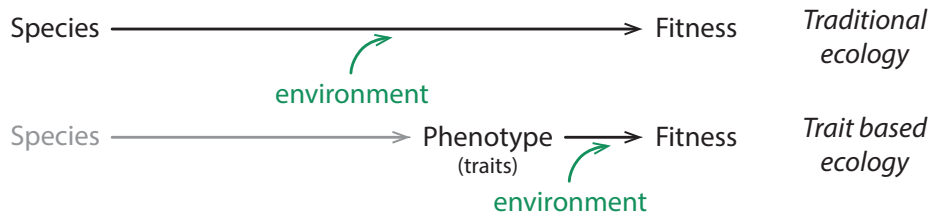


Figure 2.1: The shift toward trait based ecology allows for the decomposition of the link between species and fitness determined by the environment. On one hand, the link between species and traits is better characterised by standardised protocols and the use of databases such as TRY (TRY). On the other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

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**

THE RISE OF FUNCTIONAL TRAITS

TRAITS AND GRADIENTS

### 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 correlation 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: size 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 : morphological 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 con-**

### LEAF ECONOMIC SPECTRUM

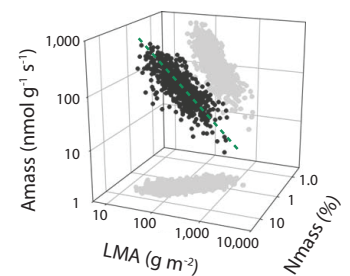


Figure 2.2: Three dimensions of the LES. Correlation of Leaf Mass Area, assimilation rate per mass unit and nitrogen concentration. This correlation reduces three dimensions (more dimensions not shown) into one axis (- -).



**straint should allow a better representation of plant functional diversity.**

### 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, drought, 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 characterization of species and communities.**

## 2.3 How traits link to ecosystem properties

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

As explained at the beginning of this chapter, 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. Com-**



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 is 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

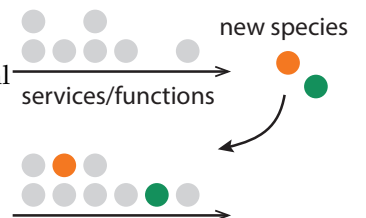


Figure 2.3: Insurance and selection effects. New species increasing diversity either reinforce existing function (●), or provide new function (●)

### 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.

However, the accumulation of trait measurements useful for the study of gradient response patterns and community structure, also reveals the variable nature of traits.

## 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<sup>1</sup>, corresponding to three different strategies: competitive (C) in low stress-low perturbations region, stress tolerant (S) in high stress-low perturbations region, ruderal (R) in low stress-high perturbations region, forming Grime's triangle (see figure 2.4).

Grime's triangle set the basis for strategy space, and the broad meaning of *stress* and *perturbations* terms allow them to be applied to various conditions. However, the diversity of types of stresses (drought, cold, nutrient availability) and perturbations (predation, fire, avalanches etc...) cannot be specifically captured by such wide concepts. Westoby 1998 highlight the difficulty to use such space and its incapacity to explain some patterns. According to him, a strategy space<sup>2</sup> 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".

#### THEORY TO TRAITS

<sup>1</sup> high stress and high perturbation regions does not allow establishment

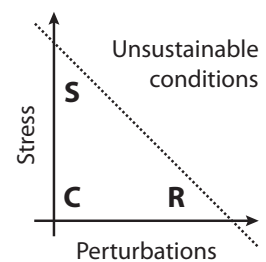


Figure 2.4: Grime's triangle. Competitive (C), stress tolerant (S), and ruderal (R) strategies are dominant in the three regions of the perturbations-stress space.

<sup>2</sup> called Plant Ecology Strategy Scheme (PESS) in his paper

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 the axis CS in Grime's triangle.
- 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 traits: DGVMs

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)

IN IBMs

#### 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 tend to ignore such simplifications procedure and relies on direct measure of traits of interest because they generally integrate a limited number of species. IBMs that can take advantage of trade-offs and simple strategy spaces to model diverse communities at small scales.

## 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

More interest in trait distribution, variability and diversity. → Get to look at **RISING INTEREST...**  
intra-specific variability.

Jung; not always in the same way (Jung, Albert, et al. 2014)

(H. Poorter et al. 2012) (L. Poorter and Bongers 2006) (Kichenin et al. 2013)  
(Siefert et al. 2015) (Albert et al. 2012) (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 it does not negate numerous conclusion from previous work, the effect of intra-specific variability on community dynamics processes must be interrogated, and underlying mechanisms investigated.**

#### 3.1.2 The effect of intra-specific variations

(Hart, Schreiber, and Levine 2016) (Courbaud, Vieilledent, and Kunstler 2010) **...AND CONTRASTING EFFECTS**  
(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

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 individual mechanisms, evolution could tackle genetic variations, phys-

iology and ecology on ontogeny, and evolution and ecology on phenotypic plasticity

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

Ecology shifted from species to traits syndromes with great success, but the intra-specific variability constitutes a great challenge for generalisation of observed patterns. By overlooking the processes that structure intra-specific variations, we might lose 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

### 3.2.1 The different sources of intra-specific variability

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?

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 <sup>1</sup> 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

<sup>1</sup> in the sense it has been selected because it provides this capacity

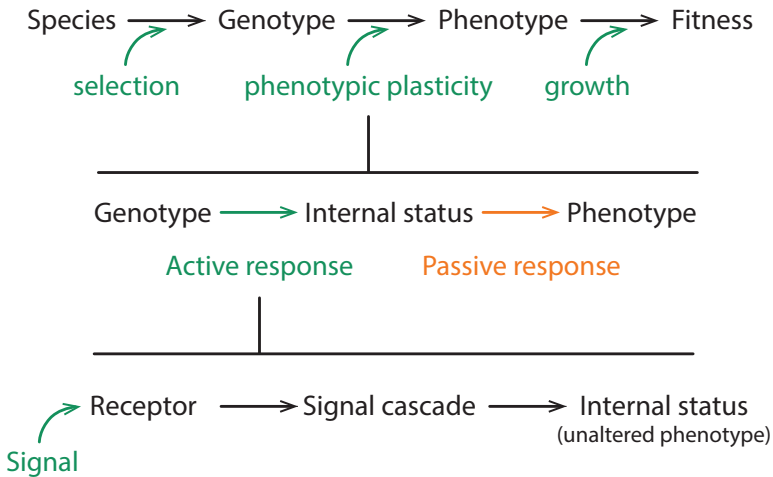


Figure 3.1: Decomposition of phenotypic plasticity as a step between the genotype and the fitness. Phenotypic plasticity is the effect of environment on the link between genotype and phenotype. Plasticity can itself be decomposed in active plastic response that change the internal status of the individual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

Active 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. Defining the extend and the rules of such mechanism is not an easy task that might depend on the context and the framework used.

#### MOLECULAR BASIS

#### 3.2.3 How to model phenotypic plasticity

what make it plastic: find the invariance. Laughlin? (what's invariance anyway) resources, but also risk (frost, grazing): alter cost and gains.

#### REFERENCE AND PLASTIC TRAITS PLASTICITY RULES: A QUESTION OF DRIVERS

### 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

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 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 ?

niche filling versus competitive exclusion: asymmetric gain and coexistence theory.

### 3.4.2 Productivity always improved?

Species able to deal with variations: stay relatively (more than without PP) when conditions doesn't match. **STABILITY**

*Pinus sylvestris* greater 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. **COSTS AND LIMITS  
DIVERSITY AND PRODUCTIVITY**

### 3.4.3 Community identity shift

### 3.4.4 Phenotypic plasticity effect on individuals and communities

**Why we need this model:**

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### III

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





## IV

### INDIVIDUAL PERFORMANCE: STRATEGY AND PLASTICITY









V

COMMUNITY DYNAMICS







VI

SYNTHESIS & OUTLOOK







# GLOSSARY

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

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

## Plasticity

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