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.

CONTENTS

I

INTRODUCTION

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

Mountain grasslands provide numerous ecosystem services

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

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. Defining and understanding the main variables that capture those links is necessary to efficiently predict changes in ecosystem services levels.

1.1.2 The facets of plant communities

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.

1.1.3 From processes to properties

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.

-

1.2 Community assembly and coexistence

Community assembly, drivers, interaction and dynamics.

1.2.1 Filtering processes: from potential to realised niche

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

PERSPECTIVES
ABIOTIC FILTERING
BIOTIC FILTERING

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

THE QUESTION 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). This set of processes are called the assembly rules. Different type of processes are at stake to maintain a community and the general filters are illustrated in the figure **??**. ...
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.
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 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

Same resources: even more difficult to understand coexistence. Must have differences on how they gather and use these resources. Species is not a handy tool to describe differences in functioning and strategies. Shift in paradigm needed.

2.1 The continuity of functional ecology

2.1.1 Shift in paradigm: traits and patterns

A shift needed

diaz, lavorel, glopnet and try

this shift worked: falster,

The rise of functional traits

Collection of multiple trait sampling.

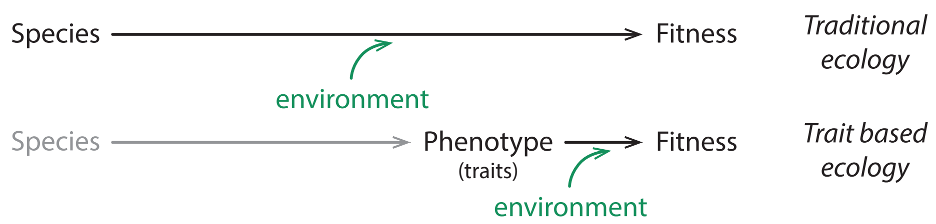

Figure 2.1: The shift toward trait based ecology allows for the decomposition of the link between species and fitness determined by the environment. On one hand, the link between species and traits is better characterised by standardised protocols and the use of databases such as TRY (**TRY**). On the 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.

TRAITS AND GRADIENTS

change of traits along gradients.

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?

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

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)

(**kunstler**)

but non transitivity: key role in maintenance diversity.

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. 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

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.

2.2.2 Strategy-spaces made of trade-offs

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.

2.3 Modelling diverse plant community

2.3.1 How strategy space open vegetation modelling

2.3.2 How models inform us on properties and dynamics

The use of strategy spaces in models allow 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. New vegetation models take advantage of the power of traits and trade-offs to model species characteristics and dynamics, therefore cannot traits be also used to describe the assemblage of these species?

2.4 How traits link to ecosystem properties

2.4.1 Mass Ratio Hypothesis and community weighted means and functional identity

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 species identity. 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.**

2.4.2 Benefits of diversity

benefit of species diversity: insurance effect - portfolio effect ?

selection, niche complementarity

functional convergence

2.4.3 Trade-offs in ecosystem properties

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.

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

Rising interest...

More interest in trait distribution, variability and diversity. → Get to look at 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 interogated, and underlying mechanisms investigated.

3.1.2 The effect of intra-specific variations

...and contrasting effects

(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

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

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?

FORMS OF 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 [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.

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

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.

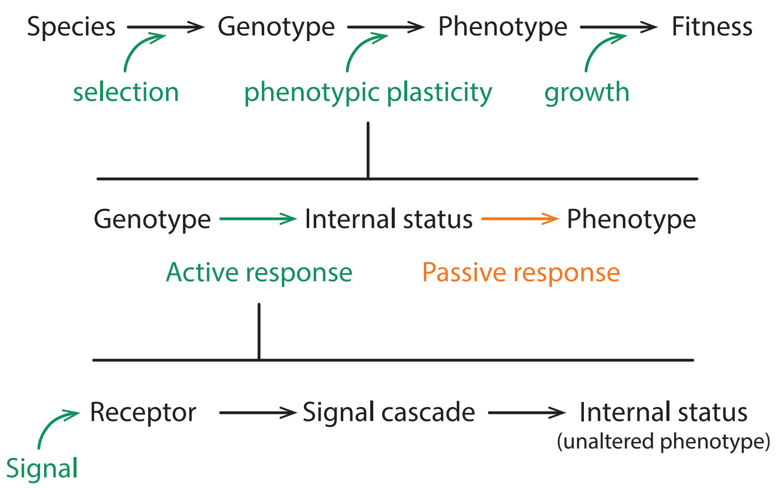

Figure 3.1: Decomposition of phenotypic plasticity as a step between the genotype and the fitness. Phenotypic plasticity is the effect of environment on the link between genotype and phenotype. Plasticity can itself be decomposed in active plastic response that change the internal status of the individual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

MOLECULAR BASIS

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.

3.2.3 How to model phenotypic plasticity

REFERENCE AND PLASTIC TRAITS

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

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 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

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.

Stability

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:

Bibliography

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.

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".

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.

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.

Poorter, Hendrik 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.

Poorter, Lourens and Frans Bongers (2006). "Leaf Traits Are Good Predictors of Plant Performance Across 53 Rain Forest Species". en. *Ecology* 87.7, pp. 1733–1743.

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.

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.

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