CLÉMENT VIGUIER

PHD THESIS

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I

INTRODUCTION

1

Objectives

1.1 Generic framework for modelling of plant communities

1.2 Effect of phenotypic plasticity on plant community dynamics

Individual level
Community response to drought event

2

LITTERATURE REVIEW

2.1 Context: mountain grasslands and climate change

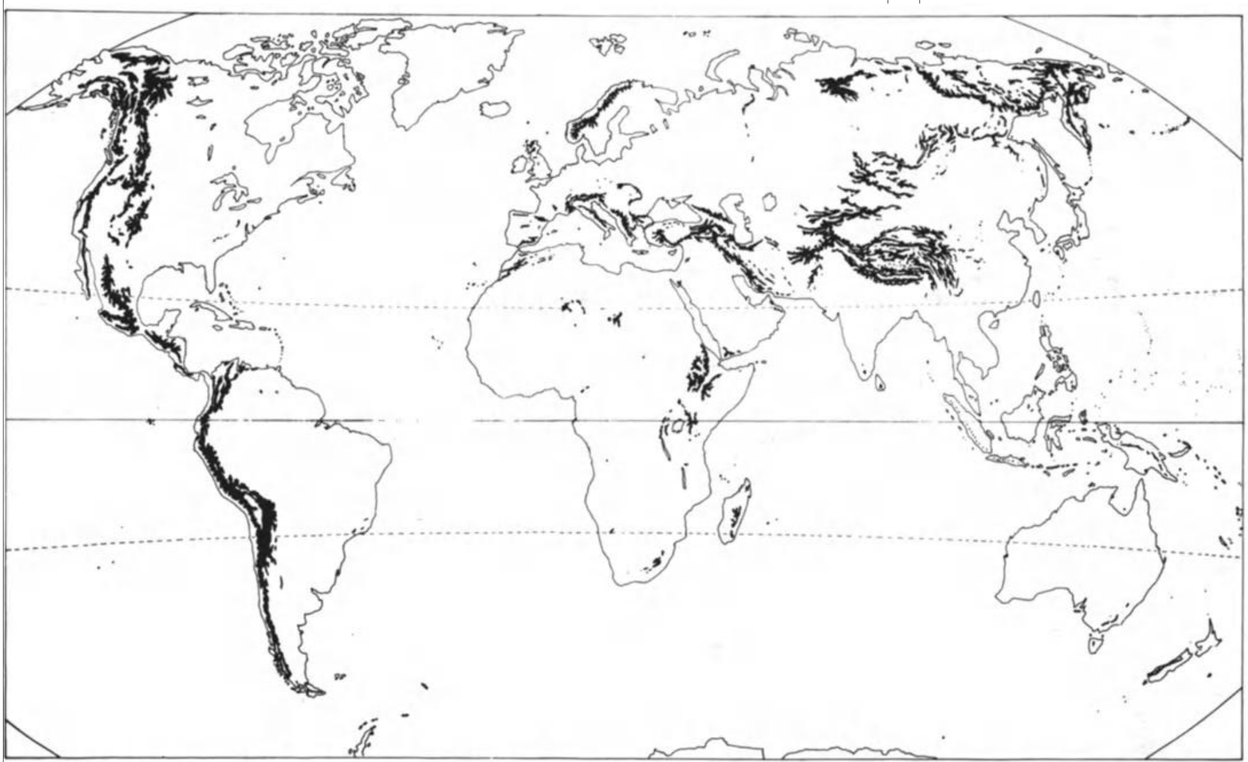

Figure 2.1: Distribution of alpine habitats

2.2 Diversity and coexistence mechanisms

Why interested in diversity? precious, main objective in conservation, plus services. Why coexistence mechanisms? Mechanism at plant level that allow diversity, understanding these will help us predict changes in diversity.

2.2.1 Effects of diversity

Conservation
productivity
resistance ?
Ecosystem services and complementarity

2.2.2 Mechanisms for coexistence

main theories: niche, neutral, individual based. -> scale and dimension dependant.
chesson Chesson (2000)
Spatial and temporal variability
trade-off, strategy space, and variability.
in the end it's rarely direct interaction but capacity to respond to stress and interect interaction through resource pools.

2.3 global change and community dynamics: theory and empirical results

2.3.1 Community dynamics: from individuals to group dynamics

Need to highligth how community dynamics emerge from individual response and interactions.

2.3.2 Intraspecific variability

frame of reference: deep traits vs shallow traits. definition of functional trait.
source of intra specific variability: genetic vs ontogeny vs plasticity (epigen)
effect on niche and interactions: effect on coexistence
-> plasticity a special form of ISV

2.3.3 Understanding phenotypic plasticity

adaptive intraspecific variation
cost and limits
effect on coexistence and community

2.4 Existing modelling solutions and approaches to question global change effect on vegetation community

Message: modelling coexistence is a challenge because 1) do not know/understand all mechanisms, 2) challenging to incorporate enough mechanisms, 3) costly computation and data wise. -> need for more generic and complete (multiple mechanisms approaches.

2.4.1 Modelling vegetation - traits and strategies

traits & strategies
existing models: a gap to fill
coexistence processes

II

MODELLING ALPINE GRASSLANDS: GENERICITY AND PLASTICITY

General framework for coexistence including phenotypic plasticity: the model ***MountGrass***

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Abstract

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1. Introduction

Global change has been subject of a large, and still growing, number of studies. Yet, because the complexitiy of ecological system coupled with the uncertainty around the future of climate and management, a lot of work is remaining to predict the state of natural and semi-natural systems in the future. Vegetation communities are of particular interest as they provide both economic value and ecosystem services. If a large part of plant community ecology is foccused on forests, the presumed vulnerability to global change of mountain grasslands has led scientists to study them. If their actual vulnerability is still discussed (phd of sandra, ecoveg 2015), mountain grasslands will certainly be exposed to increasing temperature and droughts, but also to changes in management practices with a reduction of grazing (ask greg, see ref in ceres baros first paper). To better understand and predict the effect of global change in these ecosystems

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[1] Since 1880.

of mountain grasslands, empiricall studies and experiments have been set. (see Jena, leca and Levine). These studies and others (Violle, albert, jung) highlight the importance of intra-specific variations in community ecology. Intra-specific variations represent around 20 and 30 percent of total variation in grasslands (see albert) and could greatly alter the species interactions and community response to abiotic factors. Considering intra-specific variations is important to better understand community dynamics (violle) and in models because they favour coexistence (Clark, Jung, Courbaud) and modify community responses (Jung). Such effects are succeptible to greatly influence the dynamic of communities facing global change by mitigating species level response, soften plant niches frontier, altering species competition. Another argument is the fact that intra-specific changes may alter directly the community response to a stress (Jung).

Moreover the role of long term evolutionary and ecological processes cannot be easilly assessed in such designs. Moreover, considering the multiplicity of climatic and management scenarios scales up the work to a limiting point.

To overcome these limitations and difficulties, modelling approaches has been developped (fate-h, samsara, taubert, lohier ...). They are either used for the retrospective studies long term dynamics from time series data, the prediction of community dynamics along different scenarios, or to interogate the underlying mecanisms of community dynamics (gemini). These models, to be able to account for changing condittions are all based on strong plant functioning processes at the scale of interest and are supported by field data through parametrisation.

Most of these models feature a fixed plant functioning where the dynamic of the community is mostly driven by, 1) the abiotic conditions, 2) the relative competitiveness of species/group specific parameters or direct competion coefficients. If 1) is essential in the context of climate change, the point 2) as main mecanism of plant interaction can be discussed as it relies on differences between species specific physiological parameters. Physiological or competition parameters are generaly estimated by direct measures or derived from dta through calibration. Both methods give estimators in what we have good confidence, however they do not allow them to vary within the group (plant functional type, species or population) they haved been difined for. The estimator produce good results and generally follow fundamental or ecological trade-offs. Yet, they do not allow for variations within the group for these parameters, as they are not strictly constraint by said trade-offs and could lead to darwinian demons, or would require calibration of this variation space. More efforts must be done in the representation of the link between chemical, anatomical and morphological traits and physiological traits that drive plant growth and plant interactions. Defining such link would authorise variations within a group while maintaining strong trade-offs between physiological traits and allowing variation and search in the strategy space... (not clear).

We stressed the importance of considering intra-specific variations, ann highlight the necessity for a link between chemical and anatomical traits to functioning traits. Not clear what is genetic variation and selection/evolutionary processes or phenotypic plasticity. Phenotypic plasticity in models: theoretical: 2 species interactions, not at community model. (Heritability ?)

There is a need for community models capable of reproducing diverse plant communities. To investigate the effect of climate change it has to incorporate mechanism of response and individual level.

Such mechanism is called phenotypic plasticity

2. Methods

2.1. Model overview

2.2. Calibration

Pot data. Pot data consists in total biomass and root shoot ration (RSR) data of ... species grown in pots by Peterson and al. (peterson). This old dataset has the advantages of being grass species grown in a described steady environment with two conditions of watering with measures of essential components of growth: biomass and RSR. The inputs used to simulated these experriment are detailed in appendix.

Individual calibration process. Bayessian calibration could not be used for the model considering the number of parameters and the simulation time. A filtering process has been implemented in R. Parameters are sampled following the LHS method (from `lhs` package) within parameter ranges (desccribed in table ...) defined from the litterature, and constraints dicted by desired behaviours from the model. When necessary the sample is log transformed. Because of strong relationship between exchange rate parameters and cost of exchagne area, exchanges rates parameters are expressed on a mass basis for sampling then transform to an area basis for the model. Phtosynthetic activity is defined relatively to the water uptake activity and water use efficiency (WUE) to avoid extreme root shoot ratios.

Once generated a first filtering is applied to save simulation time and avoid unrealistic trait values (see table for ranges extracted from LES data in alpine biome) that are not tested against calibartion data.
Once the parameters transformed and filtered, simulations matching growth conditions in Peterson experiments.
Generated data from finished simulations (i.e. plant lives until the end and do not exceed model's internal size limits) are then compared to experiment data species by species. Parameters of logistic distribution are computed from species

means and standards deviantions for RSR and total biomass. The use of this distribution form is justified by the intrinsic form of RSR measure and the need to reject negative values for total biomass. A parameter set is accepted for one species if it within a 95% range of the calculated distribution for both RSR and total biomass in wet and dry conditions.

Field data. Field data has been collected between years 201 .. and 201 in two distinct datasets from Chalmandrier and al.() and Claire Deleglise and al. ().

2.3. Simulation setup

3. Results

3.1. Growth of diverse species

calibration

sensitivity analysis

1d gradient: distribution of as and memory of surviving species.

niche

3.2. Plasticity in this framework

compare algorithm.

effect of tau on growth (same parameters but with no plasticity cost)

plastic calibration

4. Discussion

5. Conclusion

using fundamental "deep" traits and memory: able to reproduce a diversity of resource use strategies. Possibility to

This framework is compatible with phenotypic plasticity

plasticity change the niche shape (and probably interactions) and may have an impact on community dynamics.

References

[?]

Appendices

6. *MountGrass* description

7. State variables, traits and parameters

7.1. State variables

7.2. Species specific traits

7.3. Parameters

8. Simulations

1

Mechanistic model for plant community dynamics centred around carbon allocation

Paper 1:

1.1 Introduction

1.2 Strategy space and allocation pools

Leaf economic spectrum + Shipley + Poorter

1.2.1 Allocation or anatomy: a choice to make

what is SLA and SRL: cost of exchange area: tissue density, tissue thickness. Poorter 2009, grace2017, Katabuchi 2017, de la riva 2016

1.3 Model overview

mechanism and stochasticity
5 types of allocation

PSEUDO-CODE AND ROUTINE ALLOCATION

1.4 Plasticity: between species memory and individual experience

1.4.1 Concepts

Genetic memory (see Sonia Sultan book for references). Selection and evolutionary processes.

MEMORY

There might be optimum. But not easy to compute, especially when you consider more complex cost and interactions. Depend on different efficiencies and equilibrium... Also, you may want to avoid efficient by risky strategies (if you wrong, or if there is a quick shift). Need for strategic traits to drive allocation more than memory.

EQUILIBRIUM AND EFFICIENCY
OPTIMUM, STRATEGY AND MEMORY

Ok but what happen with optimisation allocation ? -> need the strategy to be tightly linked to memory. But that part has requirements: memory is a reliable source for strategy. Ultimately the resource availability is only one (ok, maybe two) dimension to phenotype optimisation. This strategy trait is necessary as other aspects of fitness are ignore (temperature implemented but not tested, grazzing vulnerability, frost damade, WUE, CO2 etc...) If you multiply mechanisms affecting the fitness you complexify the fitness landscape and allow for multiple strategies to be explored. Otherwise you must aartifically constraint.

This is crucial to discuss this important aspect of strategic differenciation emerging for processes and how plant change strategy as the projection of environment evolves. Memory then plays more a role of sensitivity (with tau).

But for the moment the partial implementation of that through the artificial but meant to disappear default strategy is making analysis and assumptions difficult. Ok, but how do you treat it ?

equilibrium, resource use, resource availability, condition estimation

Important role of condition estimation. Perception mechanisms. (cost). Difference between plasticity and acclimation and epigenetics.

CONDITION ESTIMATION

1.4.2 Implementation

Why the use of a sampling method: complex effect of allocation and complex allocation system that is meant to be extended. Some results on the stability of phenotypes. How sampling method can drive the allocation.

1.4.3 comparison of different algorithms

full plasticity : freschet 2015 in poorter & Ryser 2015 the two sides of the performance/fitness: equilibrium and tissue efficiency
age vs biomass.

1.5 Parameter filtering and sensitivity analysis

Obj: give confidence in the model, demonstrate is able to reproduce simple growth pattern.
Obj2: have a beter idea of plasticity on growth. growth plastic and non plastic parameter filtering: can we distinguish species thanks to species specific parameters instead of shared parameters.
does plasticity make it easier ?
Impact of plasticity related parameters.

1.6 Community dynamics parametrisation

Obj: demonstrate that the model is able to reproduce community dynamics (as it was designed for).
Find parameters that allows coexistence (suggest plasticity should allow a diversity of strategy). SLA and height data. Phytosociology for 10m quadrats.

2

Results: Model's properties and individuals response

(Related to the notions cited above, like performance decomposition)

2.1 Craft a trade-of and phenotypic map

Can memory be related to strategy and active/structural ratios in shoot and roots ?

2.2 Niche response

Obj1: understand how resource use mechanisms and allocation algorithms shape the environmental potential niche in the context of the model.
H1: strategy and memory affect niche in two ways if we suppose they are independent: shape and position. Strategy mostly affect shape (width and height) while memory (and so root:shoot ratio) affect mostly position.
H1': there is strong link between strategy and memory in the case of optimisation allocation that increase niche height and might reduce its width.
Obj2: understand the role of plasticity on the niche and if the effect in the same for all strategies/memories.
H2: the plasticity increase niche width but not height (as phenotype is optimum at the center of the niche where memory match the resource availability).

Stability and efficiency trade-off. Niche heigh and width and relationship with the strategy. How does plasticity affect that ? Does it increase the height and widen niches ? What does that mean for coexistence ?
Hopefully higher niche would go with unstable niche.

2.3 Transitivity and competition

1 vs 1 interactions
Is the resource competition transitive ? How does niche widening impact that, does plasticty change competition interaction. Is it related to the trait distance ? (don't think so)

3

The effect of phenotypic plasticity on plant community dynamics

Hypothesis on the cumulative effect on niche and interactions.

3.1 Individual resistance and resilience against drought events

Amplitude and length of the event :
- severity effect reduced by lower tau ?
- resistance versus resilience: H0: conservative strategy have higher resistance, H1 : low tau allows for re-equilibrium and increase resistance (low amplitude and long length. H2: high tau allow to avoid dead-end situation during short severe drought (high resilience)

3.2 Community response to drought event

coexistence effect vs resistance/resilience effect
uniform vs heterogenous (plasticity wise) community response H1:

III

SYNTHESIS & OUTLOOK

This section is meant to include thoughts and ideas on how to extend mountgrassbut that could not be included in the first versions of the model for various reasons. Despite not being included, these extensions are interesting from a scientific or technical point of view, and I hope these notes can be useful to anyone interested in mountgrassor individual based vegetation modelling.

3.3 Notes

3.3.1 On modelling

Frustration: often look obvious, at least it's just logical, there is what we put in...

Modelling approach, when not for prediction, what is it about ?

- building understanding
- weight mechanisms
- test hypothesis

4

Include nitrogen: source of trade-off

As seen previously in chapter , the emergence of trade-off in growth strategy in the actual framework actually rely on a strong genetic constraint over plant plasticity. Indeed, without plasticity cost and low reactivity there would be a high rate of phenotypic convergence of individuals from different species. This is explained by the existence of optimum carbon partitioning (for a given size) in a stable environment. The coexistence of different resource use strategies (exploitative vs conservative) is allowed only through temporal variations and non equilibrium state. This is quite common since a lot of models will predict rapid dominance of one entity in case of equilibrium (need references here).
Multiple questions arise from this observation: are the conclusions of this work still interesting in the understanding of the coexistence mechanisms? (I hope I did convince you in the dedicated part of this document, see .. for more details), is it possible to see coexistence of multiple strategies in a temporally stable environment? how can we produce trade-off by including only one more resource?

In the following paragraphs I try to answer these questions with theoretical arguments and suggestions on how to integrate them in MOUNTGRASS.

4.1 Stable coexistence: the need for a resource dependent tissue efficiency

Coexistence mechanisms are listed and detailed in the introduction of this thesis (see chapter **??**). Here I focus on the efficiency of tissues... Nitrogen based, why coexistence ? different phenotype correspond to different limiting resources and for different resource availabilities, different phenotype will optimize the return cost of tissues.Nitrogen also allow the model to have an extra dimension into strategy: WUE (local scale) versus NUE (global scale) (element of reflexion in Maire's thesis).
Its also can be related to

5

Specific resistance carbon pools: diversify strategies (and memory)

Original idea was to have specific carbon pools for different function, and weight the relative allocation based on gain projections.

6

Land-use: a important driver

6.1 Proto-model of management

Mapping, digestibility and selectivity (smoothing). Grazing and mowing. Height correction.

6.2 Individual and collective response

Response could be to grow thinner, more fragile leaves to go back on tracks (and take advantages of nutrients and lower competition) or grow bigger leaves and invest in predation resistance/avoidance.

6.3 Remaining questions

Calibration of herbivory pressure.

7

LOCAL ADAPTATION AND EPIGENETIC: BETWEEN SPECIES AND INDIVIDUAL MEMORY

8

MAKING IT ALL FUN

Making it fun to use, so that people use it. Making it pretty ?

8.1 Documentation and vignette

8.2 Fun and simple simulations

8.3 Theme and shiny ?

Bibliography

Chesson, P. (2000). Annual Review of Ecology and Systematics 31, 343–366.

IV

RAMBLING

9

EVOLUTION, PHYSIOLOGY AND JUSTIFICATION