

The individual basis of plant coexistence in mountain grassland and the effect of phenotypic plasticity: investigation with 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 complexity of ecological system coupled with the uncertainty around the future of climate and management, a lot of work is remaining
5 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 focussed on forests, the presumed vulnerability to global change of mountain grasslands has led scientists to study them. If their actual vulnerability is still discussed
10 (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).

[☆]Fully documented templates are available in the elsarticle package on CTAN.

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¹Since 1880.

To better understand and predict the effect of global change in these ecosystems of mountain grasslands, empiricall studies and experiments have been set. (see
15 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
20 better understand community dynamics (violle) and in models because they favour coexistence (Clark, Jung, Courbaud) and modify community responses (Jung). Such effects are succceptible 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
25 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
30 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
35 of community dynamics along different scenarios, or to interrogate 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.

40

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 competition

coefficients. If 1) is essential in the context of climate change, the point 2) as
 45 main mechanism of plant interaction can be discussed as it relies on differences
 between species specific physiological parameters. Physiological or competi-
 tion parameters are generally estimated by direct measures or derived from data
 through calibration. Both methods give estimators in what we have good confi-
 dence, however they do not allow them to vary within the group (plant functional
 50 type, species or population) they have been defined 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
 55 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).

60

We stressed the importance of considering intra-specific variations, and high-
 light the necessity for a link between chemical and anatomical traits to func-
 tioning traits. Not clear what is genetic variation and selection/evolutionary
 processes or phenotypic plasticity. Phenotypic plasticity in models: theoretical:
 65 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

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**How is it really different from source-sink approaches ? Or func-
 tional equilibrium ?** - Allocation based, trait variations, plasticity is a strat-
 egy. This last point is important. It's related to the discussion around van
 Kleunen and Dewitt (not all species are plastic, Sultan says most are) - check that.

The need of mechanistic model integrating functional traits and carbon allocation ... [?] + probably general reviews on vegetation modelling

2. Methods

2.1. Model overview and concepts

80 *Overview of MountGrass.*

Plasticity in MountGrass: concepts and implementation. **Allocation** Why allocation and not just traits ? Allocation model provide structural constraint for plant strategies. Study ecology is studying the relative performance of individuals (and their impact on environmental conditions) in relationship with their
85 strategies. Considering the amount of traits and strategies plants can develop, it is crucial to reduce the dimensionality of the strategic space (space define by all independent strategic axis plant can be found on). The most effective way to use laws of physics, chemistry and biology to eliminate impossible strategies (or combination of traits). Allocation based model take advantage of the "law of
90 mass balance" ... to limit the number of possible allocation pattern, or strategies. This approach has the advantage of creating limited *continuous* strategy space that can be explored and reveal ecological relationships/constraint. The search for such relationships or trade-offs is a big challenge in empirical ecology (see [1, 2, 3, 4] for plants) and ecological modelling (see [5, 6]) as they reduce the
95 complexity and help understand the main mechanisms that shape communities.

Plasticity: expected environment -> phenotype, here phenotype is equivalent to biomass partitioning, that means expected environment -> allocation coefficients. Then memory -> expectations -> allocation. Because low dimensions, and we want diversity, and the link between memory and allocation might
100 not be a function (one memory give exactly one optimum allocation), in the model this relationship is not verified. Species specific traits are used to allow

for different strategies to be associated to a same memory (different plants won't have the same strat, despite sharing the projection)

105 **Allocation algorithms**

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
110 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 filter-
115 ing 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
120 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.

125 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.

130 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
135 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.

Strategy diversity filtering. To further reduce the number of parameter sets considered, we proceeded in an additional filtering step. Because the first filtering
140 was conducted for only one strategy over the whole 4D strategy space (l_ini, w_ini, as_s_d, as_r_d) it is necessary to verify that other strategies do not lead to potential Darwinian demon. This should be limited by the choice of priors, while at the same time promoted by the selection of parameters increasing
145 growth to counter balance potential unfitted strategies².

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

All common parameters for pot simulations. i.e. weather, soil, default
150 species parameters.

3. Results

3.1. Growth of diverse species

Individual calibration. . Calibration filtering results in the selection of n parameter sets over m preselected parameters sets. Accepted sets are distributed
155 among the 11 species of the dataset like presented in the table. Species A, B and C are the most numerous.

²Better do that beforehand than after... But I guess it's too late now.

sensitivity analysis. The models about seems to be sensitive to the following parameters: r_1 , β_0 , P_{max} , u_{max} , k_{or} , ρ_{ar} . The four first parameters are related to global resource availability and directly related to growth rate, while the second and the last three and related to the below-ground resource foraging and exchange rate.

Total biomass is particularly sensitive to exchange rate parameters, but also tissue construction cost. (not shown)

Plasticity does not change the acceptance rate in any form (only slight increased from 0.26% to 0.38%). Despite non overlapping (around respectively and third and a quarter of accepted parameter sets are shared between non plastic and plastic calibration) the distribution of not shared parameter sets are very similar and does not show any clear pattern.

Acceptance rate without plasticity: Acceptance rate with RSR plasticity for

	species	nb accepted	rate
1	<i>Silene acaulis</i>	227	0.02
2	<i>Trifolium dasyphyllum</i>	271	0.03
3	<i>Geum rossii</i>	51	0.01
4	<i>Thlaspi alpestre</i>	342	0.03
5	<i>Deschampsia caespitosa</i>	0	0.00
6	<i>Eriogonum umbellatum</i>	500	0.05
7	<i>Townsendia scapigera</i>	593	0.06
8	<i>Astragalus whitneyi</i>	1570	0.16
9	<i>Lupinus lobbii</i>	678	0.07
10	<i>Erigeron peregrinus</i>	1	0.00
11	<i>Oxyria digyna</i>	0	0.00

equilibrium:

Change of relationship between parameters and acceptance rate -j, none

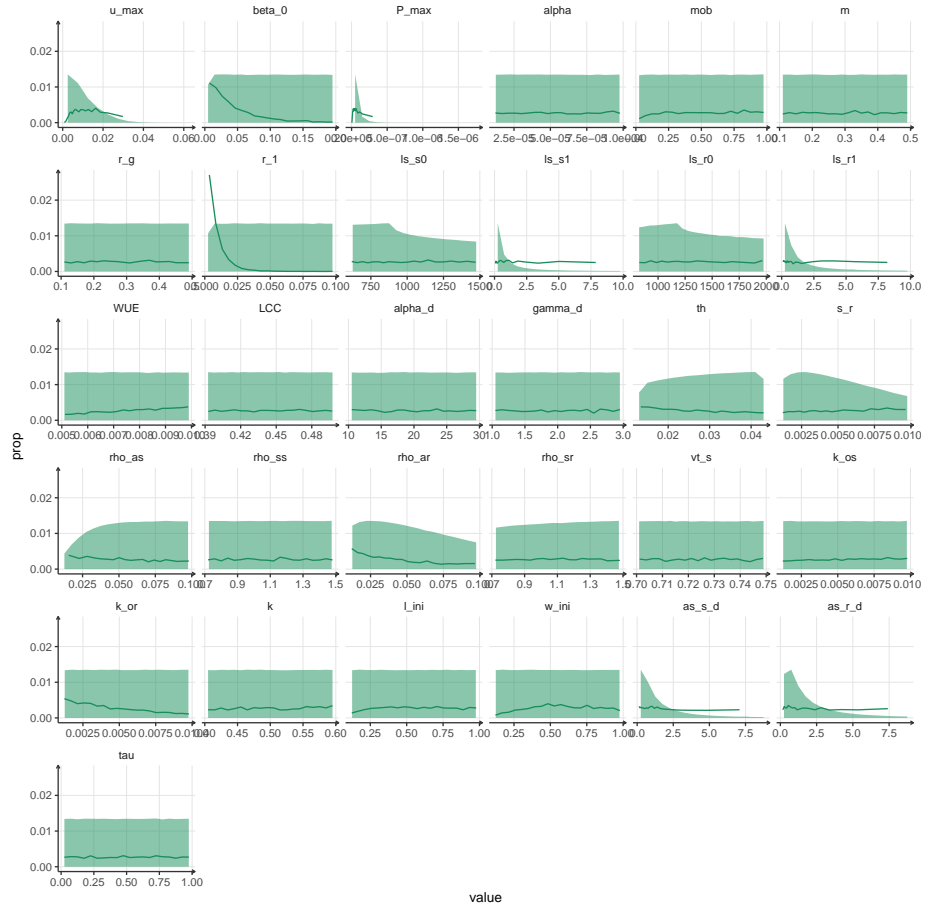


Figure 1: Acceptance rate per parameter for individual growth. No plasticity

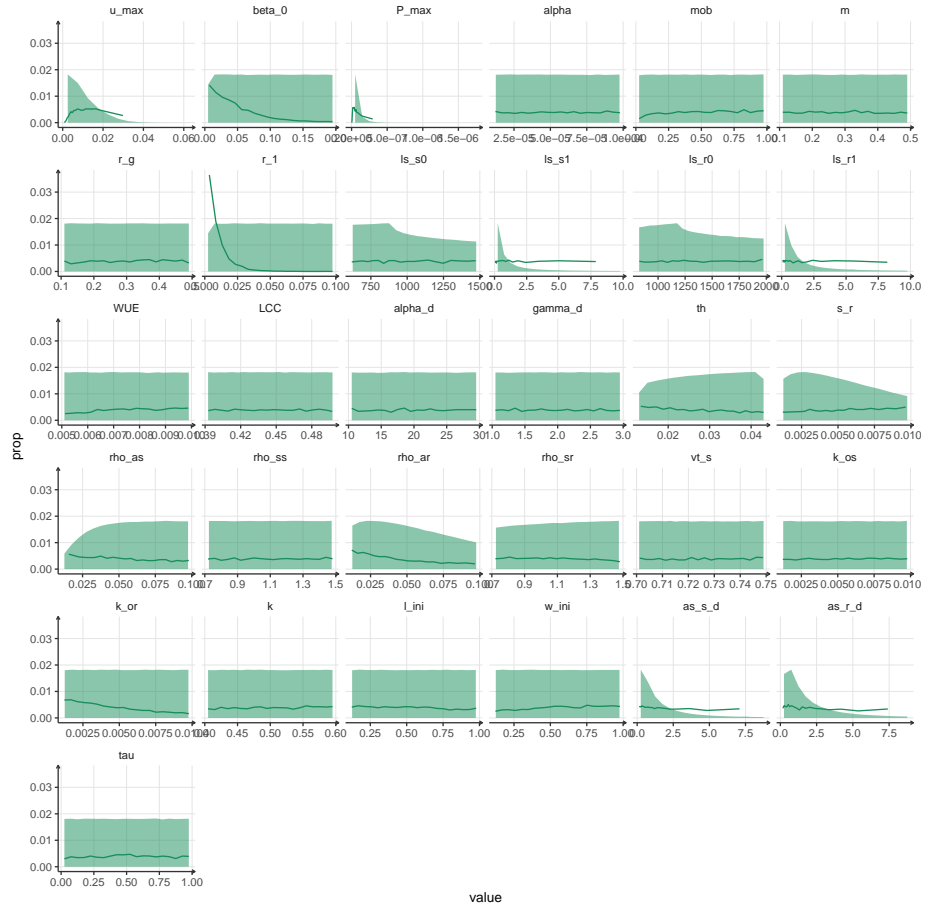


Figure 2: Acceptance rate per parameter for individual growth. RSR plasticity

	species	nb accepted	rate
1	Silene acaulis	396	0.04
2	Trifolium dasyphyllum	317	0.03
3	Geum rossii	72	0.01
4	Thlaspi alpestre	360	0.04
5	Deschampsia caespitosa	0	0.00
6	Eriogonum umbellatum	805	0.08
7	Townsendia scapigera	930	0.09
8	Astragalus whitneyi	2424	0.24
9	Lupinus lobbii	868	0.09
10	Erigeron peregrinus	0	0.00
11	Oxyria digyna	0	0.00

accept = f(tau)

175

PCA reveal that sensitive parameters are also the dominant variables in the main components of the component analysis of the accepted parameter sets. Species cannot be distinguished on the two main component space, neither on 1 or 2D species specific parameters space (l_ini, w_ini, w_ini vs l_ini, as_s_d, as_r_d, as_r_d vs as_s_d) despite small variations in distribution shapes between species.

180

Individual growth pattern and plasticity. Individual growth and allocation looks like that:

change in size of different pools (shoot, active, shoot str, stem ..., rep, storage).

185 Plus constant traits.

Different allocation algorithms change the growth but also the traits: BMtot, RSR, SRL and SLA of the same plant with different algorithms, other things being equal.

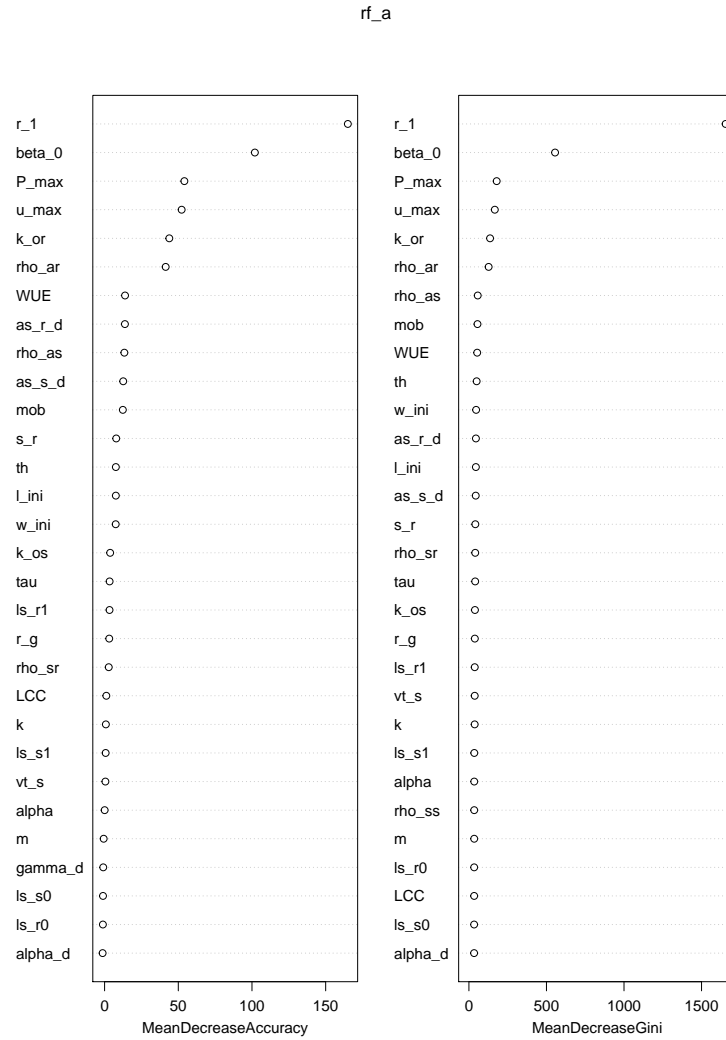


Figure 3: Importance of the random forest to explain filtering outcome (accepted or rejected) of a balanced sample of parameter set between all tested (all accepted parameters and an equivalent sample in rejected parameters). RSR plasticity.

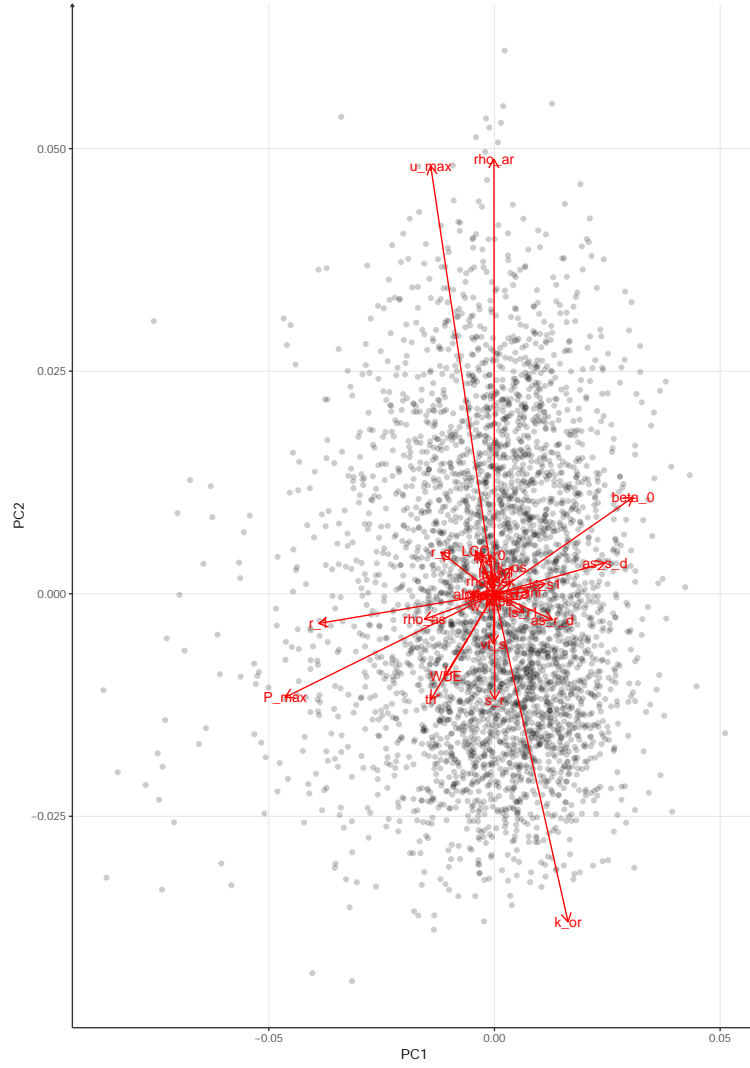


Figure 4: Accepted parameters set for plastic individual growth calibration filtering on the two main components of PCA.

190 *Active versus structural: the foundation of the niche.* Niche results from the absolute (potential niche) or relative (realised niche) performance of individual plant along environmental gradient. Performance (if measured as living biomass at a given time) in **MountGrass** is a composite variable depending on: the absolute efficiency of the different organs (shoot and root), the relative proportion
195 of these organs, and the equilibrium between shoot and root activity.

Theoretical performance trade-off: result from the mathematical expression of construction cost of tissue and their exchange rates.

figure and formulas Realised trade-off

figure and formulas

200 *Allocation matters: stability vs risk.* Effect of algo on performance → why plasticity is important: not only good allocation is important, but also good measure of conditions.

(there is some conceptual drawing to put in here: optimum landscape and how can allocation let you drive in that space.)

205

Freer allocation algorithms lead to convergence to phenotypes of higher performance. But these phenotype may also be of higher risk ! →

4. Discussion

Individual calibration. Individual calibration allowed to filter parameters related to individual growth with only few parameters being sensitive.
210

individual growth. Link memory and phenotype.

Link allocation algo and plasticity to the different components of performance.

5. Conclusion

215 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.

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Appendices

6. *MountGrass* description

270 7. State variables, traits and parameters

7.1. *State variables*

7.2. *Species specific traits*

7.3. *Parameters*

8. Simulations