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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

II

BACKGROUND: COMMUNITY DYNAMICS, TRAITS AND PHENOTYPIC PLASTICITY

III

MODELLING ALPINE GRASSLANDS WITH MOUNTGRASS A GENERIC FRAMEWORK INTEGRATING PHENOTYPIC PLASTICITY

IV

INDIVIDUAL PERFORMANCE: STRATEGY AND PLASTICITY

1 MODEL PROPERTIES AND INDIVIDUAL RESPONSES

The modelling framework developed in previous chapter offers multiple options to explore the effect of phenotypic plasticity on plant growth, and later plant community dynamics. Before investigating the effects of such mechanisms on complex systems dynamics, it is important to have a deep understanding of the model behaviour at individual level. As explained in introduction, the relationship between resource and individual plant growth is the base for plant interactions, abiotic filtering and coexistence mechanisms. This chapter of the document focuses on the calibration and exploration of the model for isolated individuals. The results of the simulation experiments exploring diverse aspect of resource-plant growth relationship will be interpreted at individual scales, but I will also attempt to extend conclusion to higher level mechanisms.

The first part of the chapter is dedicated to the parameter filtering process, the sensitivity analysis and basic model behaviour. Then follows the exploration of plant performance as a function of plant strategy and resources levels and dynamics.

1.1 Parametrisation and sensitivity analysis

Calibration, or , is an essential step in the development of an agent-based model. ABMs are often characterised by multiple processes, and though parameters, at individual levels. The results of these processes (depending of parameter values) from numerous individuals combine to produce the group or community behaviour. Because there are interactions between the processes and between the agents, the overall behaviour of the group (often the subject of interest) is sensitive to these parameters. For the same reasons, an incredible variety of results could be produced with ABMs if the parameters where not chosen in order to produce sensible responses to simulated conditions. The aim of the calibration is to determine, from the *a priori* knowledge of the processes and parameters, and the comparison with data, the best values for the model parameters. This step often goes along with a sensitivity analysis that determine the relative sensitivity of variables of interest to specific parameters.

Because of their nature, ABMs often model processes for which the parameters are either unknown, or hard to access (because at the individual scale). In such cases, advance calibration techniques like pattern oriented modelling[hartig; Gri+05] can be developed. However, such method require a high number of simulations and relatively precise simulation parameters. Because the implementation in R makes the model relatively slow, and because available datasets, despite being very interesting lack information on sensitive parameters, a less robust but less expensive approach is chosen: at the individual scale. The fo-

cus of the part of this work on the individual growth, and the will for more individual-centric approach also support this choice.

For similar reasons of computational cost, the is realised *a posteriori* on calibration runs.

1.1.1 Method

Pot data consists in total biomass and root shoot ration (RSR) data of 11 species grown in pots by Peterson and Billings [PB82]. This 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.

POT DATA

Simulated plant grow in square pots 9 cm wide and 12 cm deep. The soil is characterised by the following parameters: critical soil water content: $0.1m^3.m^{-3}$, and saturation water content: $0.1m^3.m^{-3}$. Simulation time of 111 days of 15 hours is divided between the growing phase of ... days, followed by the treatment phase when plant are water (soil saturation) either once a week or once a day. The light level and water influx are simulated with water event of ... mm and lighting of ... Watts per square meter. Plants have default geometry parameters and reproduction is ignored and I assume plants do not stop their growth.

POT SIMULATION

The whole filtering process has been implemented in R. Model parameters are sampled following the LHS method (from `lhs` package) within parameter ranges (described in table ??) defined both thanks to the literature and constraints dictated by desired behaviours from the model. When necessary the sample is log transformed. Because of strong relationship between exchange rate parameters and cost of exchange area, exchanges rates parameters are expressed on a mass basis for sampling then transformed into an area basis for the model. To avoid extreme RSR ratios, the ratio between the mass based exchange rate parameters is limited between 0.1 and 10.

PARAMETER FILTERING PROCESS

As explained in previous chapter, species specific parameters are requited to model plant growth. These parameters are sampled at the same time that the parameters of the model, according to ranges detailed in table 4.2.

Once the parameters generated, a first filtering is applied to save simulation time and avoid unrealistic trait values. Compute initial trait values considered out of range (see table for ranges extracted from LES data [Wri+04] in alpine biome) are excluded.

These two steps lead to the creation of a list of n independent parameter sets that are then used for individual pot simulations following Peterson and Billings experiment sett-up.

Results 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 deviations 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.

The parameter filtering procedure is applied on the three main allocation algorithms: *non plastic*, *fixed-equilibrium* and *plastic-optimisation*.

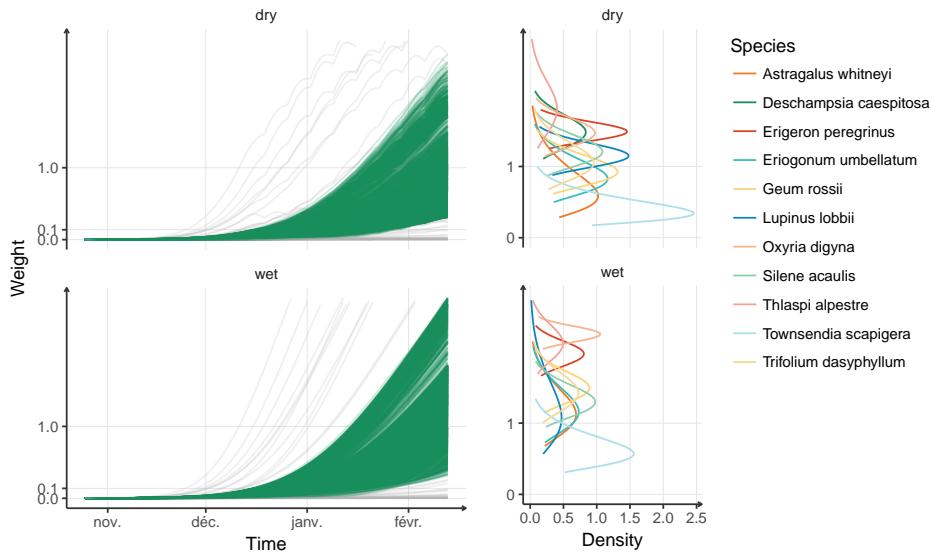


Figure 1.1: Comparison of simulated weights with distribution of weights of real alpine species for contrasting conditions.

Relative importance of variables in the selection process is investigated with the packages `randomForest`. A random forest analysis (depth = 5, number of trees = 300) is performed on a balance dataset composed by all selected parameter sets and a random sample of rejected sets of equal size. Importance is assessed on the results of the random forest.

SENSITIVITY ANALYSIS

1.1.2 Results

Parameter filtering process resulted in the selection of a low number of parameter sets (below 0.2%) for each allocation algorithms (table 1.1.2). This number is below the sum of accepted parameter sets per species because a parameter set can match to multiple species. Not all species contribute to the same extend to the filtering process. *Astragalus whitneyi* accounts for a high percentage of accepted parameter sets, while no parameter set could match 2 species (*Oxyria dignya* and *Deschampsia caespitosa*). The former is characterised by wide distribution in both conditions for the two variables of interest (weight and RSR), while the latter show relatively tight distribution with little overlap between the conditions for the both variables (see figure 1.1 for comparison between simulations and data for total weight).

SELECTION RATE

Despite the low selection rate, a difference can be noted between the *fixed-equilibrium* algorithm and the two other algorithms with a accepted rate of 0.14 % against 0.09% and 0.10% (table 1.1.2). This difference cannot be explained by a significantly better selection rate for specific species, but rather higher rates for all species.

Most of parameter sets are not shared between the algorithms (*i.e.* around respectively and third and a quarter of accepted parameter sets are shared between *non plastic* allocation and *fixed-equilibrium* allocation calibrations), despite that the distribution of parameter values that are not shared are very similar and do not show any clear pattern (data not shown).

Out of the 31 parameters, 6 show graphical response of selection rate (see figure 1.2), and only *u_max* and *P_max* present a possible optimum different from

Table 1.1: Acceptance rate per species for the 3 main allocation algorithms. Because some parameter sets match multiple species, the total number and rate of accepted parameter sets is lower than the sum of accepted parameter sets per species. All rates are given in %.

| species | non plastic | | fixed-eq | | plastic | |
|------------------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | n (2M) | rate | n (2M) | rate | n (200,000) | rate |
| Silene acaulis | 227 | 0.02 | 396 | 0.04 | 55 | 0.03 |
| Trifolium dasypphyllum | 271 | 0.03 | 317 | 0.03 | 45 | 0.02 |
| Geum rossii | 51 | 0.01 | 72 | 0.01 | 12 | 0.01 |
| Thlaspi alpestre | 342 | 0.03 | 360 | 0.04 | 59 | 0.03 |
| Deschampsia caespitosa | - | - | - | - | - | - |
| Eriogonum umbellatum | 500 | 0.05 | 805 | 0.08 | 118 | 0.06 |
| Townsendia scapigera | 593 | 0.06 | 930 | 0.09 | 107 | 0.05 |
| Astragalus whitneyi | 1570 | 0.016 | 2424 | 0.24 | 318 | 0.16 |
| Lupinus lobbii | 678 | 0.07 | 868 | 0.09 | 123 | 0.06 |
| Erigeron peregrinus | 1 | <0.01 | - | - | - | - |
| Oxyria digyna | - | - | - | - | - | - |
| Total | 4233 | 0.43 | 6172 | 0.62 | 837 | 0.42 |
| Accepted | 924 | 0.09 | 1416 | 0.14 | 200 | 0.10 |

limit values. The relative importance of the parameters is better explored in sensitivity analysis.

A total of 12 parameters show relative influence on selection rate for at least one of the algorithm. These parameters are divided between model parameters and species parameters. Species parameters show influence only for the *non plastic* allocation algorithm. Model parameters express relatively similar importance for all three algorithms. The respiration rate of active tissues (r_{-1}) is the most sensitive parameters (see figures 1.2 and 1.1.2). Other sensitive parameters are related to water availability (β_0), organ exchange rates (P_{\max} and u_{\max}) and soil coverage by roots (ρ_{ar} and k_{or}).

SENSITIVITY ANALYSIS

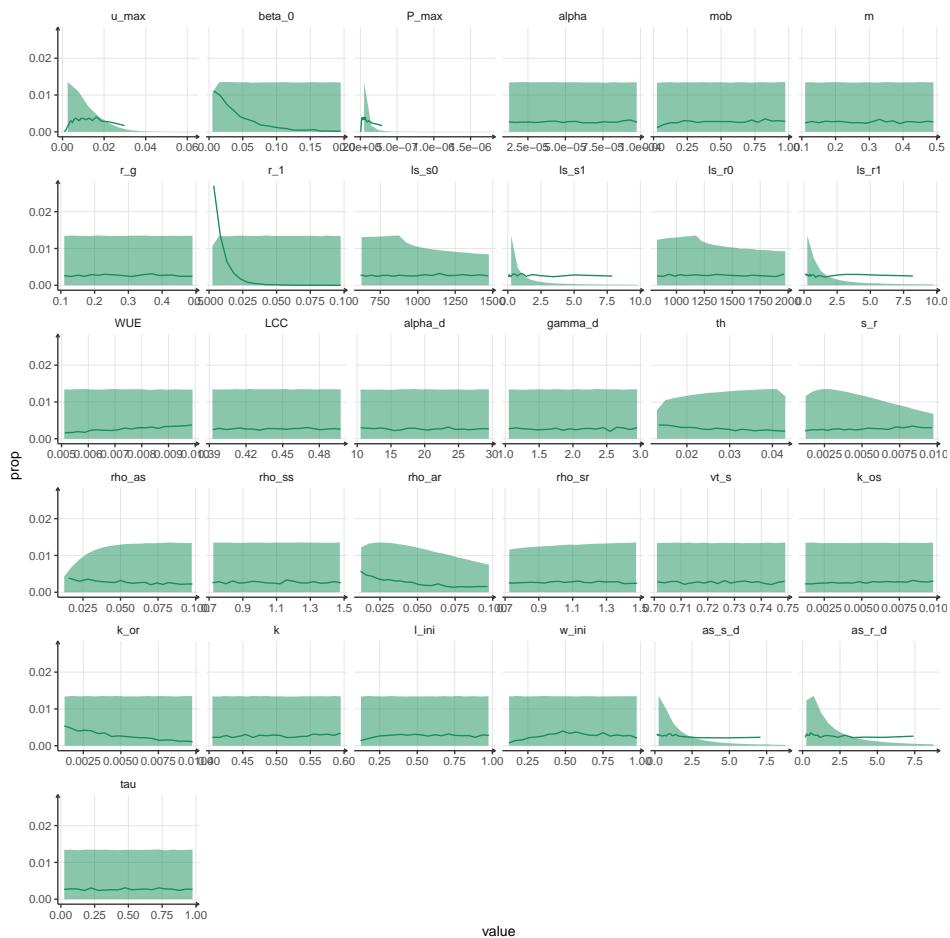


Figure 1.2: Selection rate per parameter for individual growth. Non plastic.

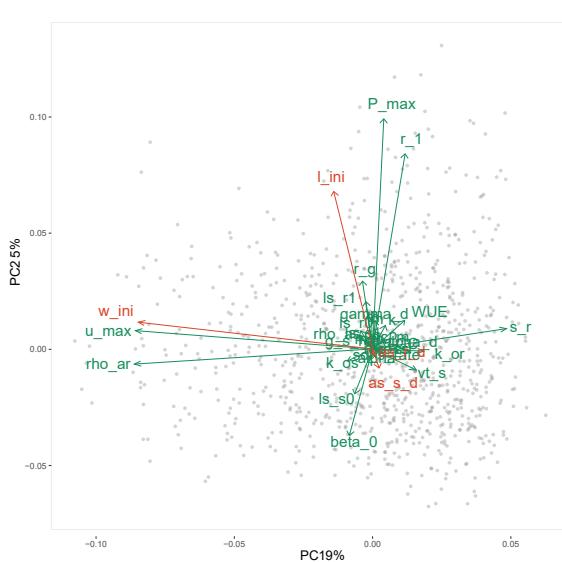


Figure 1.4: Representation of the PCA of parameter sets selected in parameter filtering process on the first principal components. *Non plastic*.

Relative mean decrease accuracy

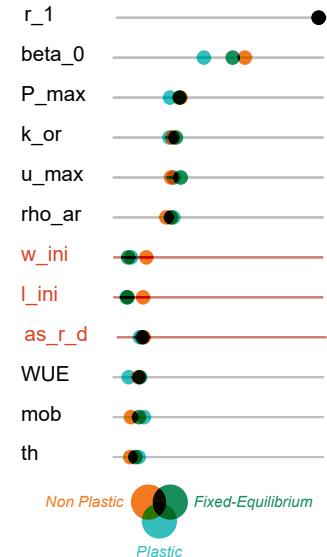


Figure 1.3: Relative importance of main parameters for selection under the three main allocation algorithms: (*non plastic*, *fixed-equilibrium* & *plastic*).

The PCA performed for *non plastic* algorithm only on parameter values reveals that important parameters are also the dominant variables that shapes the selected subspace. The two first axis explain only 14% of variance. The first one is related to the root activity and efficiency (u_{\max} , l_{ini} , ρ_{ar} and s_r), the second is in line with global efficiency and resource availability.

The parameter filtering process is based on individual species, ... Species cannot be distinguished on these two main component space, neither on species specific parameters space (l_{ini} , w_{ini} , w_{ini} & l_{ini} , $as_{\text{s_d}}$, $as_{\text{r_d}}$, $as_{\text{r_d}}$ & $as_{\text{s_d}}$) despite small variations in distribution shapes and ranges between species (data not shown).

For each algorithm the response of the two filtering variables (weight and RSR) are plotted against the most important variables in figures 1.5 and ??.

VARIABLE RESPONSES

Total biomass is particularly sensitive to tissue respiration cost (r_1), but also maximum exchange rate parameters. There is a notable difference in growth maxima between the two conditions in favour of wet conditions, in line with observed data. This difference is observed for the three algorithm that differ mainly by the amplitude of the biomass ranges (need data). Growth response curves are similar for all allocation algorithm. Growth is only weakly related to species specific parameters. Total biomass under *Plastic-optimisation* algorithm seems to be more sensitive to variables influencing the exchange area per unit of biomass.

The species specific parameters τ controlling the balance between genetic and environmental control does not emerge as a influencing parameter at the global scale for any of the two flexible allocation rules.

Root:Shoot Ratio (or RMF in figure 1.6) strongly responds to species specific parameters under *non plastic* allocation because the memory parameters (l_{ini} and w_{ini}) are the means plants control their RSR. For other allocation rules, species specific parameters have little control over RSR. Surprisingly, the photosynthetic capacity has stronger influence on the ratio than the root maximum exchange rate.

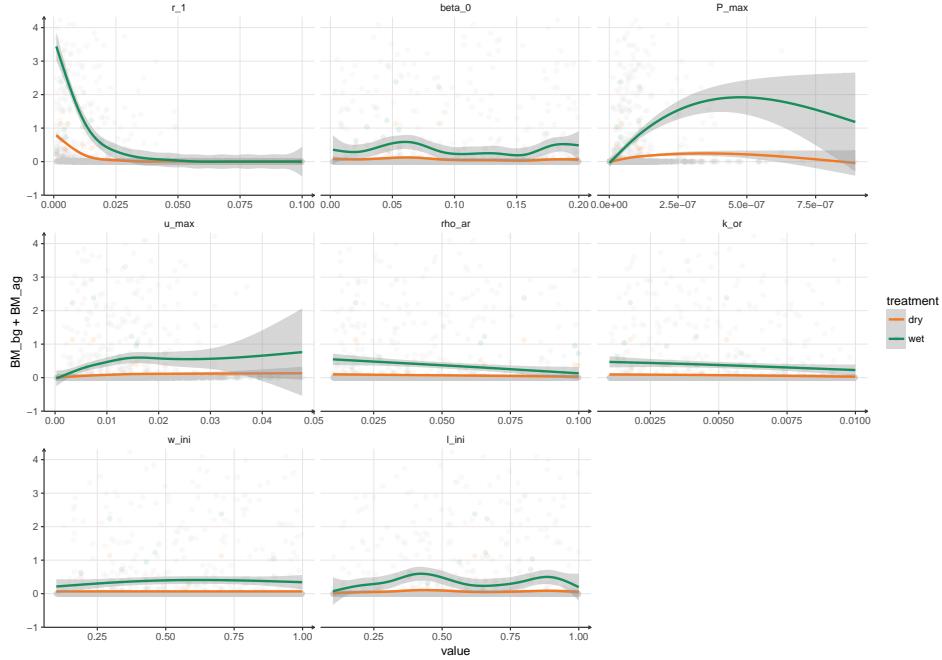


Figure 1.5: Main parameters effect on the total plant biomass. Non plastic. One dot represents a parameter set. Not all parameter set are represented as the y axis is limited around the smooth function (loess). Coloured points represent selected parameter sets in the two treatments (**dry** and **wet**).

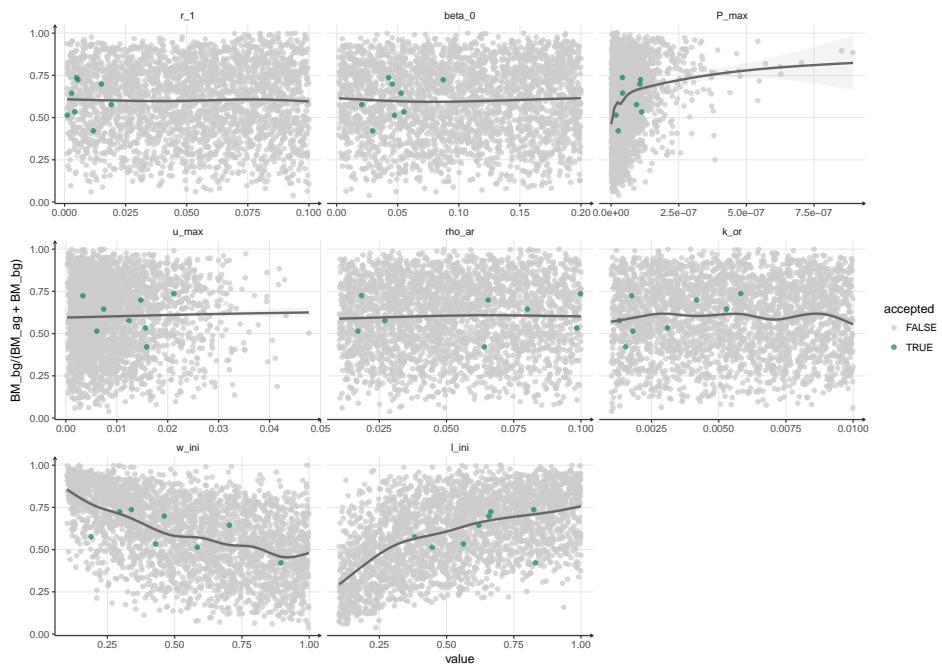


Figure 1.6: Main parameters effect on the total plant Root Mass Fraction (RMF). Non plastic

Little to no difference in RSR is expected for *non plastic* allocation rule since allocation promoted a fixed phenotype, but both *fixed-equilibrium* and *plastic-optimisation* allocation rules allow for changes in RSR. Nevertheless, no stable change in RSR is observed in any of the simulations. Fluctuations are present but consist in stable oscillations between two fixed values (see figure 1.7), synchronized with water variations. These rapid adaptations of the relative proportion of roots denote a high flexibility of plant phenotypes in *MountGrass*.

ROOT SHOOT RATIO AND PLASTICITY

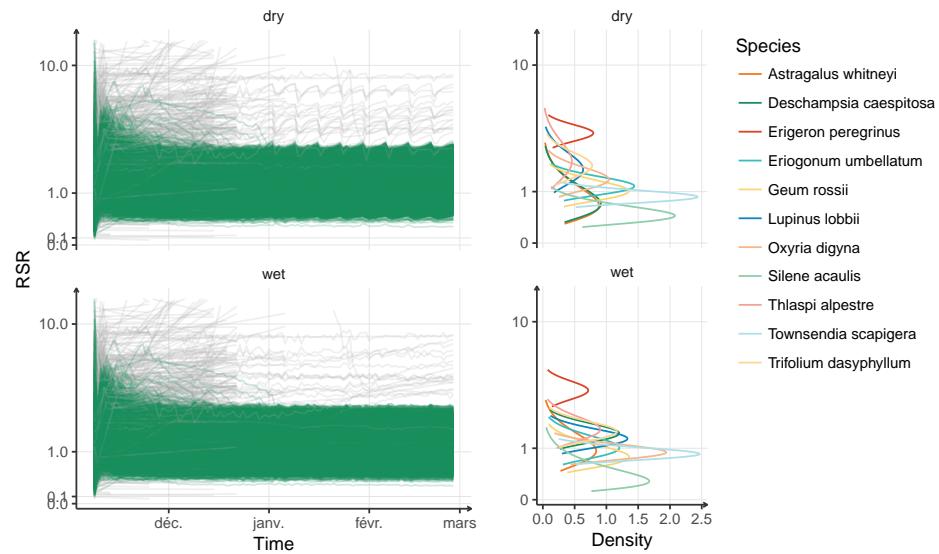


Figure 1.7: in two contrasting conditons. Because there is no plasticity or ontogeny, the simulated plant do not express any chagnes in RSR.*Fixed-equilibrium*.

1.1.3 Discussion

The relative low selection rates for all allocation rules highlight the complexity of fitting such complex model to empirical data, despite the relative simplicity of the data. This difficulty seems to lie in two factors: the high number of parameters and the lack of stable changes in RSR. This last point is further discussed in the following paragraphs. Nevertheless, plant growth is reproduced in two contrasting conditions for multiple species, and while plastic algorithms have a greater potential for growth (more high growth rate), this is not systematic and the absence of clear pattern for the most influencing parameters, such as maximum exchange rates and respiration rates, indicates that such high growth depends on a combination of parameter values. I believe that the shape of gain and cost functions along the functional trade-off between active and structural tissues plays a determining role in the growth. A trade-off function with a wider viable range is more likely to be selected as more strategies would grow (therefore reducing the relative sensitivity to species specific parameters). Considering the exponential shape of the turn-over function (one of the main cost with respiration), the width and height of the trade-off (or net gain function) is probably more strongly linked to the gain functions (exchange rates) and linear cost function (respiration), explaining little effect of parameters related to lifespan (already preselected otherwise). There is a strong dependency between viable strategies (and as a consequence functional potential diversity) and the main trade-off between resource acquisition and efficiency.

GROWTH AND STRATEGY SPACE

Filtering the parameter sets based on all species instead of individually would have been ideal to quantify this link and better calibrate the model. However, such approach would have required many more simulations, when the parameter filtering method was chosen for its low computational cost. Moreover, considering the number of species specific parameters, fitting the strategy subspace (at least default active tissue allocation parameters, memory of resources and stability) of 11 species to the data in combination with more than 20 models parameters is near impossible. Ones should have had first determined the relative positions of the species within the said strategy space before any global calibration routine. Nonetheless, species specific parameters have an influence on model main variables. Memory parameter affected the RSR in the context of *non plastic* allocation rule (see figures 1.7 and ??, while the default proportion of active tissues in roots was an influencing parameter in all algorithms (figure 1.1.2, `as_r_d`). Therefore, they should be analysed in further simulations within the same set of model parameters.

Change in modelling paradigm. Bayesian paradigm where the information is contained in data and revealed by the structure of the model. Go for simulation experiment approaches where the model is used as a simulation tool and results as new data. The emerging patterns inform us on the impact of the modelled mechanisms (even if they do not totally match the data). Model as an understanding tool.

Growth is reproduced, but only for one species, not full strategy space.

If the parameter filtering step did not result in the selection of optimum values for all parameters, it provides information on the main mechanisms influence plant growth. Indeed, the relatively high importance of parameters related to water shows the importance of the resource on the model behaviour. Both water availability (water absorption limitation, exchange rate) and root mass and construction parameters are important to match the empirical data. Considering that the calibration relies on experiment data of drought events, it is no surprise that parameters related to water economy show strong influence on the selection rate and model behaviour. In the context where the model has been developed, water shortage is expected to an important factor in community dynamics. In this perspective, the ability of *MountGrass* to reproduce the difference in productivity in both conditions, and the relative sensitivity to water related parameters is an advantage. The link between water resource, species strategy, plant performance and phenotypic plasticity is explored more in details in the following section.

THE ROLE OF WATER

Sensitivity of different variable to the parameters make sense and align with the two criterion of selection (that work with the independence of trade-off).

As mentioned earlier in this discussion, the model is not able to produce any shift in RSR in different water treatment. It is not a surprise for *non plastic* algorithm, but the filter was still applied on this criterion to allow the comparison with plastic algorithm and to be able to measure the improvement in selection rate. However, even plastic algorithms do not show strong enough response to water treatment in term of RSR. A strong and good (in the sense it would have matched the data) is larger in amplitude and more stable in time. Such processes

MORE COMPLEX PLASTICITY?

generally amplify with time, *i.e.* when the number of drought event increases, the response (allocation to roots) increases (relative to default phenotype). Unlike natural systems, plants in *MountGrass* fluctuates between two "states", or phenotypes associates to the dry and wet conditions. The RSR post drought event is reached after the first week without water. This can be explained by two main mechanisms that are related but have contrasting implications. The quickness in response to the changing conditions is allowed by relatively high assimilation rate. If the net growth rate is controlled by the total weight condition during the filtering process, the assimilation rate is not and can be compensated with relatively high turn-over rate. Net growth rate being equal, species with higher assimilation rate will have higher phenotypic flexibility (higher fraction of biomass to invest in carbon pool of choice) than species with lower assimilation rate. This flexibility, similar to reallocation, allows changes in RSR, but not the accumulation of biomass in roots. Unfortunately, both the constant turn-over rate implemintaed in the model, and the selection toward "wide and high" gain functions limit control on this aspect.

Moreover, the fact that plants are more productive during periods where they may not want to invest in roots strengthen this effect. Indeed, a plant would drift to higher RSR if it was more productive when pursuing the high RSR phenotype than when pursuing the low RSR phenotype. This last point mentions the "will" of the plant, in the context of *MountGrass* this target phenotype is encoded in the projection of external conditions. Because this projection is daily based by design, the accumulation of drought stress is not translated in the internal projection variables of the plant (like it can be with the accumulation of phyto-hormones [need ref]). This limitation highlights a big difference between simulated plants in *MountGrass* and natural plants. While solutions to overcome this problem can easily be imagined(see equation ?? in ??), they would require more parameters and introduce more complexity to the analysis. This model provides a first approach to phenotypic plasticity in grassland models and the formulation of the projection, key element of the phenotypic plasticity, is certainly a starting point for further development. Nevertheless, the differences in response to the parameters between the three allocation rules, despite shared plant functioning, demonstrate the importance of plasticity itself. And simplification of the processes should not be a reason to not explore its effects. The fact that the parameter tau has a relatively small impact on selection rates also support the need to better understand all strategic axis before focusing on the effect of projection. While there are many ways of simulating the phenotypic plasticity, the parsimony is privileged. This simple representation is enough to understand the effects of active plastic allocation in association with the other strategic differences between species.

Root shoot ratio changes were not captured by the model. The structure of the plasticity mechanisms does not work with the given watering cycle. Needs to add one parameter for reactivity.

1.2 Individual level behaviour and properties

Calibration and sensitivity analysis give information on the main processes of plant growth, but the general effects of the allocation rules on plant growth are not fully identified. In addition, because the parameter filtering processes

was limited to individual plants, and the response of species specific parameters dependent on other parameters of the model, the effects of these species specific parameters should further be investigated. The objective of this part is to set better understanding on the role of and species on plant development as basis for interpretation of plasticity effects in following chapters.

The challenge of the framework presented in paragraph 2.2.1 under *plastic-optimisation* is to control the phenotype with the values of the memory. The risk of this approach is to have too tight estimation function of the fitness (or driving function) and to see the convergence of all species (with different memory values) toward the same phenotype (same allocation of active and structural tissues in roots and shoot). The extend to which different species memory lead to different phenotypes under full genetic control (non influence of external conditions) is explored through simulation experiment under *plastic optimisation* allocation algorithm.

1.2.1 Method

The effect of allocation on phenotypic development is investigated thanks to pot simulations (see Methods in 1.1) of 100 days in 3 watering treatment: 2mm, 8m and 16mm per day. To avoid drift in the phenotype due to allocation algorithm (see paragraph 2.2.1 on phenotypic determination), simulations where run a first time, then rerun with default specific traits matching traits at the end of the first simulation set. All four algorithms are simulated.

ALLOCATION ALGORITHMS

Memory plays a determining role in phenotypic development under "plastic" allocation rules. The effect of this memory alone (environmental cues ignored by setting tau to 1) on the default emerging phenotype is explored for diverse memories (9 values on the two axis from 0.1 to 1 later scaled to the maximum area exchange rates for model parameter set considered, or 81 values) for each accepted parameter set. The effect of the memory values on the final position of plants in the phenotypic space are visualised by fitting loess curves.

MEMORY & PHENOTYPE

1.2.2 Results

think of a "showtime" visualisation that shows how growth and traits are impacted by allocation rules and tau.

ALLOCATION RULES

The kinetic of the phenotypic shift is first visualised for one parameter set on the two main phenotypic axis (proportion of active tissues in roots: PAR and proportion of active tissues in shoot: PAS). From the same starting point the five species show distinct rapid shift toward segregated subspace of the 2D strategy space. The equilibrium point is reached in 10 days.

MEMORY AND PHENOTYPE

Strong effect with saturation: optimum.

There is also a positive effect, that is smoother and have lower values. Same pattern for light memory respectively with proportion of active tissues in shoot, and proportion of active tissues in roots.

1.2.3 Discussion

Allocation rules are extremely important as they reduce the phenotypic space explore. Without even considering plasticity. Need a good understanding of

ALLOCATION RULES, PLASTICITY AND PERFORMANCE

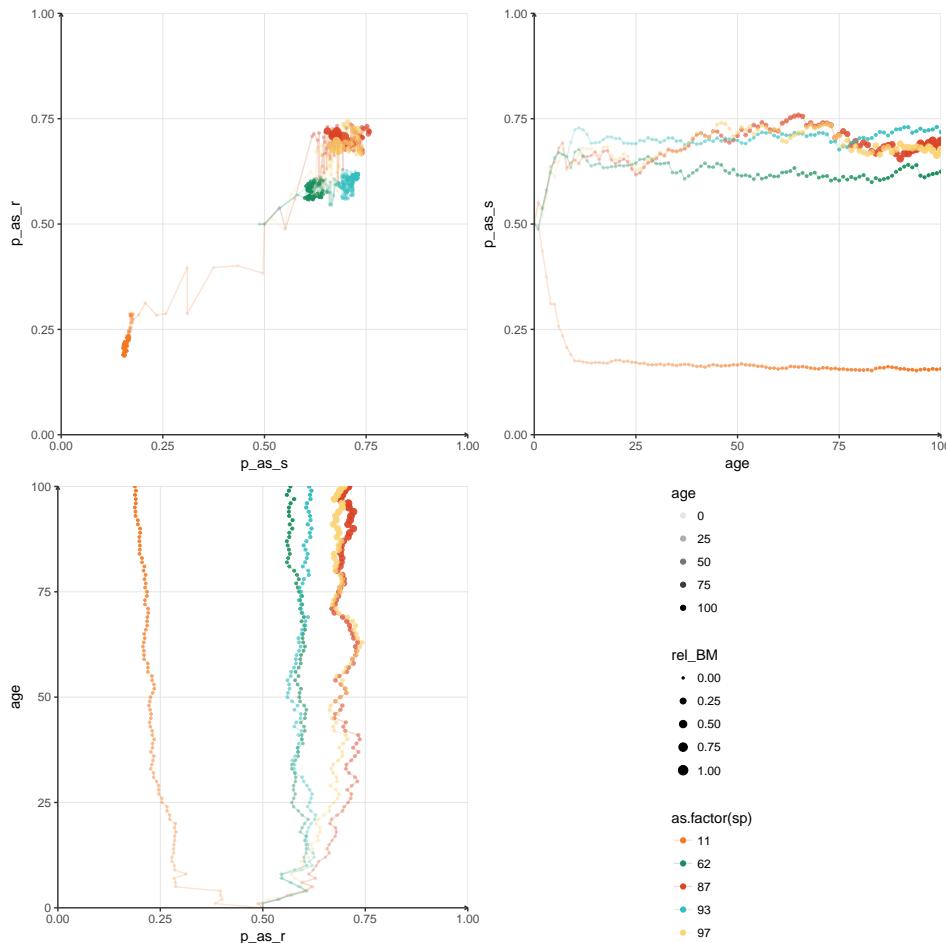


Figure 1.8: Trajectories along time in the strategy space of 5 plants with different memories. After 10 days, all plants have converged toward the estimated optimum.

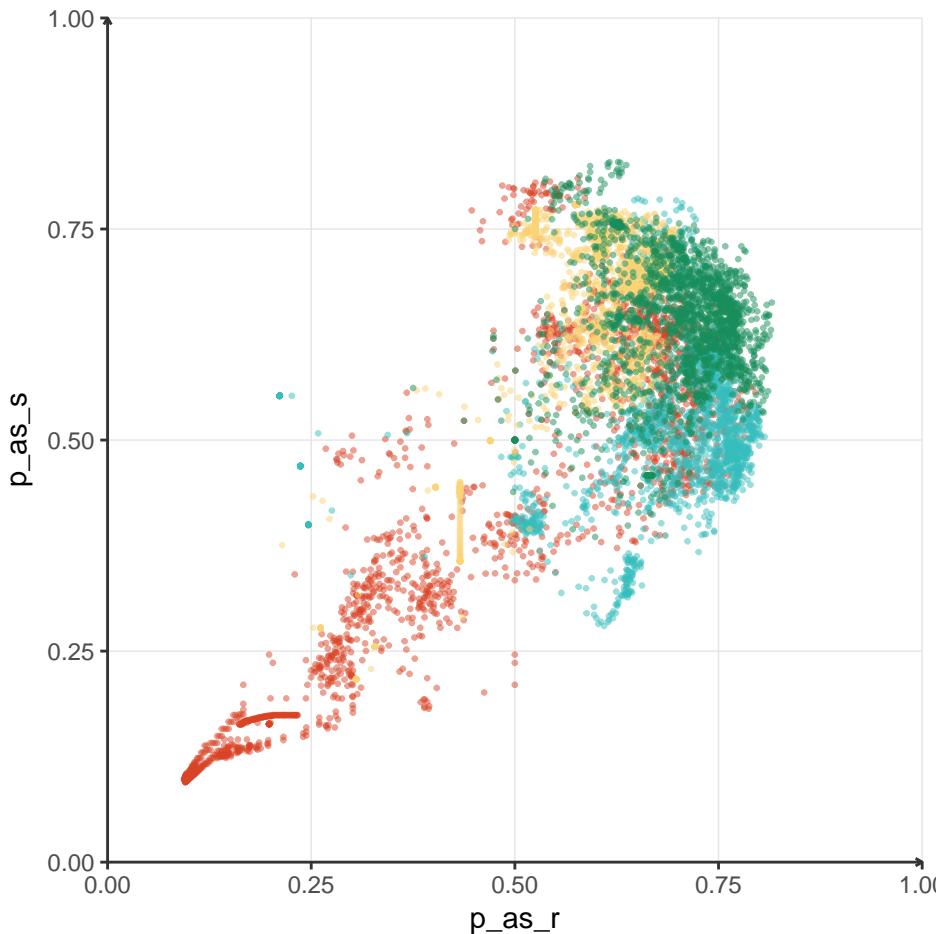


Figure 1.9: Impact of species memory on final phenotype in case of fully plastic allocation. Each point corresponds to a plant phenotype for a memory syndrome for a given parameter set. Colours denote the memory syndromes.

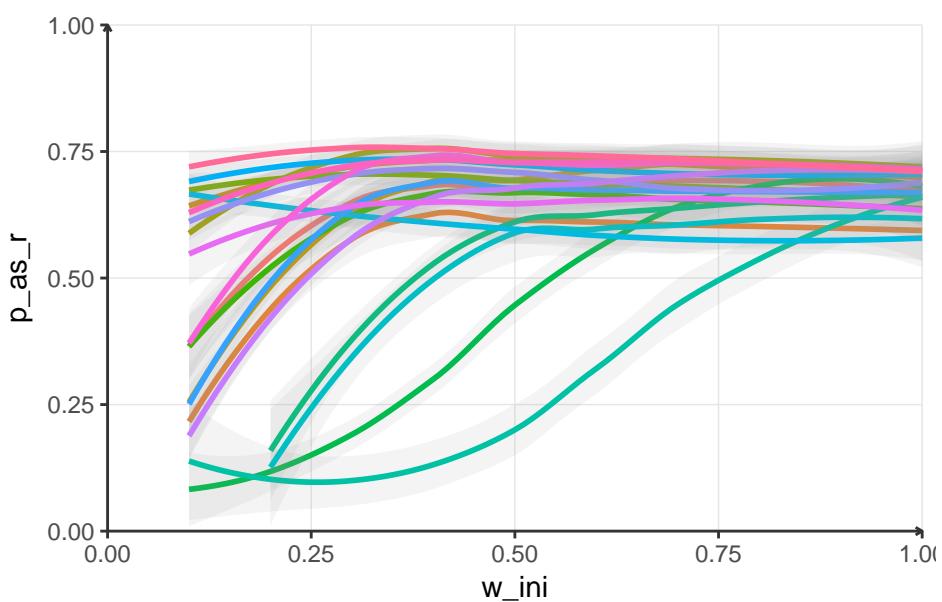


Figure 1.10: Effect of memory of water availability on proportion of active tissues in root.

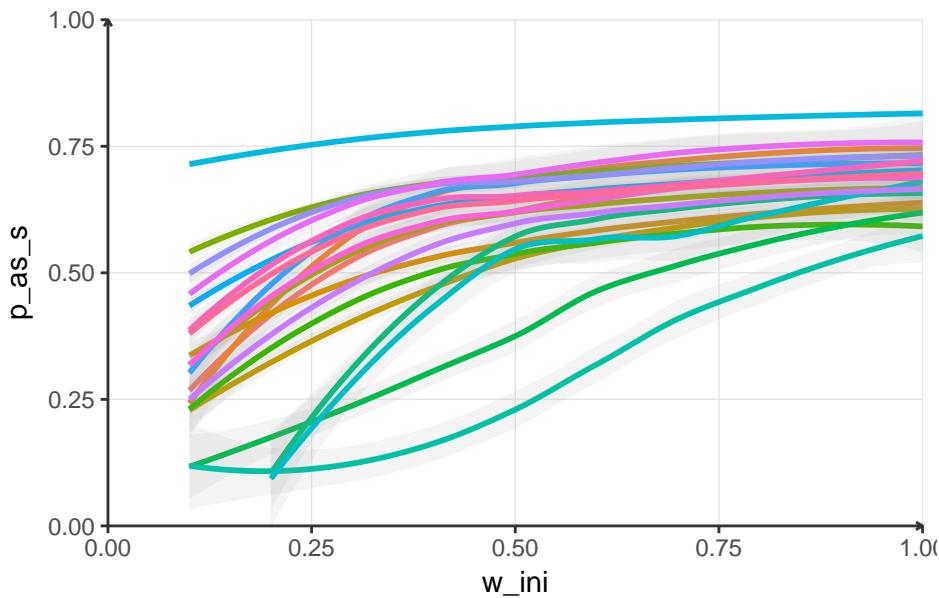


Figure 1.11: Effect of memory of water availability on proportion of active tissues in shoot.

the performance within the phenotypic landscape. Plus there is a need for alignment between starting phenotype and endpoint. Will also affect how plasticity is driven.

... nothing here, the idea was to show that the "strategy" of the species conduct to slow and fast archetypes.

Allocation trade-off allow for strategies from the fast-slow spectrum to arise, independently for shoot and root, in coherent framework. Potential effect of other strategy axis can be analysed alongside this trade-off, even if they affect composite traits like SLA or SRL.

The symmetry and the curves shapes suggest that resource related organ is more sensitive and that "apparent" increase in resource availability promote more exploitative strategy.

For each parameter set the alpha shape of the volume could be drawn to have an idea on how parameters impact potential functional diversity.

Memory is a strong enough driver to control plant organ strategy. The effect of overall activity should be studied too and considered if memory is used to determine the default phenotype.)

FAST SLOW STRATEGY AND ALLOCATION TRADE-OFF

MEMORY AND PHENOTYPES

2 INDIVIDUAL PERFORMANCE, PLASTICITY AND VARIABLE CONDITIONS

2.1 Individual performance: between strategy, memory and plasticity

Question I try to answer: (use of schematics ?)

2.1.1 Method

Idea, having an idea on how the

Two climatic conditions. ... Watts per square metters and .. mm, days of 15h.
Low resource availability conditions correspond to a reduction by a factor 4 of
resource influx, but the day length was conserved.

STRATEGY SPACE SAMPLING

SIMULATION SET-UP

2.1.2 Results

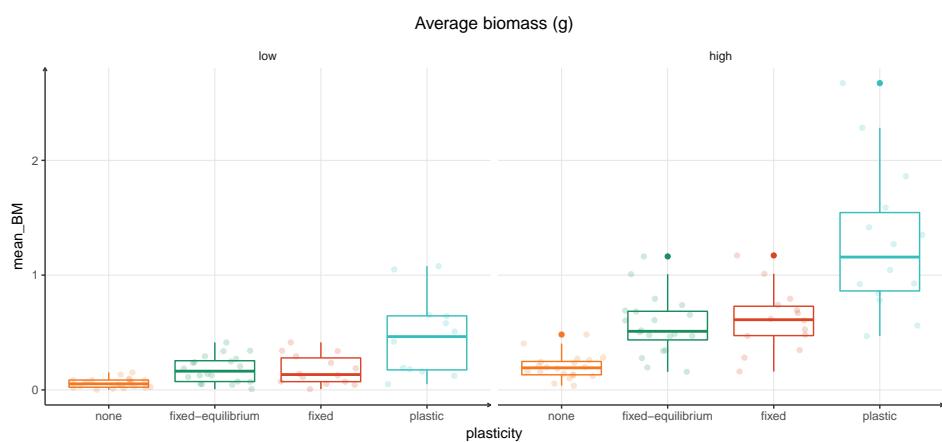


Figure 2.1: Effect of plasticity and resource availability on average biomass of living species.

Biomass is relative to best performing non plastic plant (to remove the general parameter set effect on growth) and compare (within each condition) the effect of allocation algorithm. Plasticity lead to an increase of average relative biomass, especially full plasticity. However, few values above 1, in fixed conditions there is real additional value of plasticity compare to fixed allocation.

Then talk about convergence. To better subspace, but not the optimum.

2.1.3 Discussion

Somehow I need to talk about the cost of being wrong. Can be observe in the delta heatmap on delta strat and delta w-init: in this case there is less impact of being wrong of memory if you're good with strategy, because your not in different conditions...

CONVERGENCE TO SUBSPACE

Potential effect on diversity: lower functional diversity, increase evenness. Leave highest fitness spot free. Why? environmental cues or gain function? Delta between projections?

Anyway, being good in stable conditions may be useless if cannot survive or keep gain in other conditions. » look along gradient if best species keep their rank.

This analysis was conducted with drastic parameters of plasticity with plastic plants relying only on their perception of external conditions to develop their phenotype. The different results ... different directions and impact on potential diversity.

The contrasting responses of the different algorithms highlight the importance of the allocation mechanism. However, the unique framework implemented in *MountGrass* creates a variety of nuanced responses that are not all explored here. But, the continuous gradient of strategy between species relying on species memory only and species following their perception of external condition should be kept in mind during the interpretation of these results and following.

results from this part

NUANCES AROUND PLASTICITY

Why we need to go for a gradient.

RESOURCE AVAILABILITY

2.2 Plasticity and variability of conditions

Question I try to answer: (use of schematics ?)

2.2.1 Method

2.2.2 Results

2.2.3 Discussion

Phenotypic plasticity

Kichenin (different response to gradient) Doesn't work in this framework: Not so sure about that: depending on your initial memory plants show directional changes toward one phenotype. Yeah, but they should have converged for other conditions too... So, it doesn't work. Might be explained by:

- different conditions: because heterogeneity and habitat selection, or changes in competition hierarchy;
- different ways to tackle changes on one dimensions;
- different weights between mechanisms impacting composite traits, because of the different traits.

IMPROVEMENT IN VARIABLE
CONDITIONS
HETEROGENEITY OF RE-
SPONSE

One of the argument to say this is new, however not really explored, neither with plasticity cost perspectives (a bit with plasticity limits) or with tau. However, used extreme cases: give better understanding and necessary before finer analysis. Still, there are hypothesis on the effect on diversity and the role in phenotypic stability (attention: isn't it just because the formulation of projection is wrong that we can make these conclusions ?).

PLASTICITY AS A STRATEGY

What about the continuous τ gradient ?

EXTENDED INTERPRETATIONS

What about interactions and cycles ?

The phenotypic plasticity implemented in *MountGrass* improve the relative performance of multiple strategies by concentrating the plant toward a subspace of higher performance for most of plants. Convergence to a smaller

subspace can be assimilated to reduction in phenotypic diversity, but it reduce performance heterogeneity and should favour local plant diversity. .. a few words on dynamics... Meta-community diversity is however reduced by the reduction of potential axis for niche differentiation. Plasticity costs and limits should play major role in the balance between these mechanisms. Community level simulations are needed to further understand the cumulative role of competition, spatial and temporal variability and plasticity costs on phenotypic plasticity influence on plant community dynamics.

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V

COMMUNITY DYNAMICS

VI

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