

Such approaches are also used to study more specific mechanisms like fire perturbations (Scheiter, Langan, and Higgins 2013). In this case, specific traits are included. The adaptive value of the traits in such frameworks thanks to the inclusion of genetic optimisation processes. This kind of approach is a first step in the understanding of the effect of drivers on community property responses. However, the large scale of these models often does not allow to look at small scales/interactions and dynamics.

*such as ...  
incomplete sentence*

Individual-Based Models are great tools to model community dynamics incorporating local interactions and small-scale dynamics. Because they are interested in smaller systems, IBMs often do not use strategy-spaces and prefer species-specific parametrisation (Soussana et al. 2012; Taubert 2014; Lohier 2016). This is often explained by the focus on heavily managed grasslands with objectives of productivity that need precise predictions and model a limited number of species. But strategy spaces <sup>have been</sup> are used in IBMs to understand diversity patterns in diverse systems such as savannahs (Reineking et al. 2006) or forest (Falster et al. 2016). These approaches successfully describe the diversity and encourage us to use such strategic differentiation spaces.

IN IBMS

Higher diversity can be achieved in these models, but numerous species can be discarded. The benefit of a smooth continuum in strategies is that it avoids strong dominance and shifts. Also, the perception of finer changes in the community is possible, while small <sup>errors</sup> default in species parametrisation of species centred models could lead to either no shift (one species dominates and is not sensitive to drivers) or drastic responses (the shift in dominance is abrupt because of no intermediary species).

#### 2.4.2 How models inform us on properties and dynamics

The term model <sup>s</sup> represent a large class of simplified representations of real systems, or conceptual ideas. These are always tools to better understand our world, it can be more by their design and their construction or more by their use (simulations). Here the focus is on simulation models, and particularly agent-based models (of grassland systems). How can these models inform us <sup>about</sup> on the real systems?

One way <sup>are</sup> the use of models can help us understanding a system is the simulation experiment. This approach is very similar to empirical experiments. The experimenters <sup>are</sup> put the system, here the model, in different conditions and confront <sup>being tested</sup> the results with the hypothetical results predicted by the theory they are testing. In this case, the model is treated as a functional representation of the reality providing the necessary properties to test the hypothesis. And the model shines here in contrast with the real system by its capacity to test large numerous <sup>a</sup> conditions <sup>at</sup> for a very low cost, both in money and time. This is for example the case of the model developed by Taubert 2014 to test the richness-productivity hypothesis. These simulation models also allows prediction/exploration of the system behaviour under alternative climate scenarios (Rodriguez, Van Oijen, and A. H. M. C. Schapendonk 1999; Scheiter and Higgins 2009). This is particularly interesting <sup>when</sup> to explore <sup>ing</sup> global change scenarios.

HYPOTHESIS TESTING

But, this requires a certain level <sup>of</sup> confidence toward the model. This confidence is acquired during the building and calibration process, that can also give <sup>both</sup> insight <sup>on</sup> the systems modelled.



a particular model, as it is a simplification of a given system, has often one perspective driven by the questions the scientist tries to answer. Because of that, the modeller tries to reproduce only a fraction of the properties/behaviours of the system. In this case, the models inform us by their capacity to reproduce the essential properties with a minimum number of features and the minimum complexity. This is helpful to identify and understand the core mechanisms that allow the emergence of a particular behaviour of the system. Reineking et al. 2006 show the capacity of simple allocation trade-offs to let emerge diverse communities, in addition to show the importance of the water (temporal and spatial distribution) as a driver of the community structure. The complexity of studied systems or organism often limits the identification of the causes of an observed pattern. Models are valuable when they have the capacity to reproduce observed patterns with a minimal complexity, identifying the necessary and sufficient components required for the behaviour to emerge. See the work of Lohier et al. 2014 on the ontogenetic shift in Root:Shoot ratio for different species. The calibration process can be necessary to gain confidence in the model, but it can also provide new insights. In particular, Bayesian techniques rely on specific information to inform on the value of the model's parameters. These specific parameters have a value to understand the biology or specificity of the species relatively to other species or the mean behaviour of the model.

MINIMAL REPRODUCTION

species rich

inclusion: all calibration techniques combine models, parameters, and data

Each of these two forms of insights come from the unique feature of simulation models: their capacity to turn on or off their mechanisms, or rather to switch between different representations of the system. This capacity offers a great flexibility and allows to understand the role of the different compartment of the system, and the likelihood of alternative mechanisms. This particular method was used for example in the work of Maire et al. 2013 to explore the effects of nitrogen on grassland communities.

ON/OFF BUTTONS

The use of strategy spaces in models allows the representation of high diversity in a common plant functioning framework, requiring a limited number of parameters. Such approaches are very useful to follow the dynamics of communities in a mechanistic framework. Individual models tend to ignore simplifications procedure and relies on the direct measure of traits of individuals because they generally integrate a limited number of species. IBMs can take advantage of trade-offs and simple strategy spaces to model diverse communities at small scales while keeping biological mechanisms at their core. Models can then be used in different ways to build better understanding of the modelled systems. However, models based on existing strategy space tend to model mean individuals and ignore the individual variations.

inclusion: you use models focusing on particular species rather than model models with strategy spaces?

THE IMPORTANCE OF PHENOTYPIC PLASTICITY AS A SPECIES



### 3.1 Intra-specific variability change the rules

#### 3.1.1 Increasing interest in intra-specific variations

*The emergence of*  
Trait approaches ~~emergence~~ lead to a better understanding of general patterns of community responses to drivers and of trade-offs in plant functioning. But with the accumulation of large trait databases, the importance of intra-specific variability could not be ignored. *often appear to assume that*

*Consequently,* The extent of the intra-specific variation is a big question as some ecologists point out, because trait-based approaches *appear often problematic* make sense only if inter-specific differences are greater than intra-specific differences. While this can be discussed, high functional variability within the species would weaken theories and generalisation based on mean traits. Violle et al. 2012 suggest that the extent of within-population variability relatively to within-community variability should be considered *and* avoid mistakes in the estimation of coexistence mechanisms. Ignoring intra-specific variability lead to underestimation of niche overlapping, plastic response to neighbours, or the fraction of resource a species can use. Multiple studies focused on the extent of functional intra-specific variability (Cécile Hélène Albert, Thuiller, Yoccoz, Soudant, et al. 2010; Cécile Hélène Albert, Thuiller, Yoccoz, Douzet, et al. 2010) and how to disentangle this variability from species turn-over (Lepš et al. 2011) in community response. These studies show contrasting results between traits and levels. Cécile Hélène Albert, Thuiller, Yoccoz, Douzet, et al. 2010 demonstrate a within-species variability explaining between 20% and 40% of total trait variance, and Siefert et al. 2015 note similar levels, but this fraction tends to decrease with the increasing community diversity. They also show that the strategic differentiation between exploitative and conservative species is robust to these variations. It appears that all traits are not variable to the same degree and traits like SLA, height, LNC and LDMC are relatively variable while leaf morphology traits variability is lower. *not* Siefert et al. 2015.)

*Effect of trait or trait?*  
The variability of multiple traits certainly impacts the functional diversity (Bello et al. 2011; Cécile H. Albert et al. 2012). All indexes are not sensitive to the same degree, with single trait measure being the most sensitive, but should be used carefully to draw an interpretation of ecological pattern linked to functional diversity. To overcome this difficulty and disentangle the effects of the different forms of functional diversity, specific indexes *have been* are developed (Bello et al. 2011).

The relative extent of intra-specific variability depends on the trait, spatial extent, and species richness, but not on climatic conditions (Siefert et al. 2015) suggesting general mechanisms.

*whether*  
The fact that some traits are variable, while others are not, implies that some mechanisms structure this variability. A way to identify such effects is to look if variability is structured along environmental gradients, suggesting adaptation mechanisms.

Along such *environmental* gradients, trait variability for traits like SLA (H. Poorter, Niinemets, et al. 2009) of leaf mass fraction (LMF) (H. Poorter, Niklas, et al. 2012) follow similar patterns as inter-specific response (Niinemets 2001), with increasing SLA along precipitation and temperature gradient, and decreasing SLA along radiance gradient (leaf mass fraction shows similar responses). These responses suggest strong constraints (similar to the ones that shape inter-specific



differences) shaping this variability. However, species may vary in their response (Kichenin et al. 2013). This contrast can be explained by differences in position around a bell-shaped response curve around the optimum (see Cécile Hélène Albert, Thuiller, Yoccoz, Soudant, et al. 2010 for more details). Kichenin et al. 2013 argue that <sup>it is</sup> not the case because alongside a wide altitudinal gradient the response curves observed for any trait or species are not bell-shaped.

This additional level of variability is not always in the same direction as community response driven by turn-over (Cécile Hélène Albert, Thuiller, Yoccoz, Soudant, et al. 2010; Kichenin et al. 2013; Jung, Cécile H. Albert, et al. 2014) leading to difficulties <sup>to</sup> predict the response of the community. These levels <sup>need to</sup> must be disentangled, <sup>have to</sup> in order to do that, mechanisms underlying intra-specific variability must be understood. This is particularly important because they have multiple effects on how we model community dynamics and understand coexistence mechanisms Bolnick et al. 2011; Violle et al. 2012.

After the emergence of trait-based ecology and its high potential, the recent focus on intra-specific trait variability questions the strength of mean species approaches. While intra-specific variability does not negate numerous conclusions from previous work, because of its large extent and how it alters functional diversity, its effects on community dynamic processes must be interrogated, and underlying mechanisms investigated.

### 3.1.2 Contrasting effects of intra-specific variations

Intra-specific variability impacts coexistence mechanisms and community properties in multiple ways. The following paragraphs are not an exhaustive list of all <sup>the</sup> intra-specific variations affect community properties or coexistence mechanisms, but <sup>present</sup> a few contrasting examples to emphasise the need for better identification and understanding of underlying mechanisms.

Hart, Schreiber, and Levine 2016 use a mathematical model to investigate the impact of intra-specific variations on coexistence. They demonstrate the negative effect of intra-specific variations by the intermediate of Jensen inequality effects, that leads to an under-estimation of competitive dominance because of the non-linearity. I argue that this problem is partially solved if the estimation of the mean parameter is empirical, in this case, the variability is taken into account. Moreover, this certainly applies to genetic variations. Indeed, the plastic response would emerge if there are changes in conditions, changes that certainly affect the competitive interactions. Such change (justifying a change in phenotype), is likely to alter the competition relationship as modelled. This supposition is supported by the fact that variations away from the mean are generally due to a distance from the optimum of the niche, and therefore, certainly a lower fitness and lower competitive ability.

The Jensen's inequality is one of the many mechanism through which the intra-specific variability can impact the dynamics of communities (Bolnick et al. 2011).

Intra-specific variations (ISVs) <sup>→ introduce abf</sup> can also greatly affect the niche, as any new phenotype is likely to be better adapted to an alternative environment. Therefore, this variability widens the potential niche of the species. In addition to have a potential large impact on the community structure and dynamics, the comparison of the different levels of variance give insights on the driving forces shaping

JENSEN INEQUALITY

unclear

how ?

all unclear

NICHE