The existence of such trade-off can be explained by constraints that shape the distribution of trait distributions. Trait-function relationships are often depicted as bell-shape with an optimum (Cécile Hélène Albert, Thuiller, Yoccoz, Soudant, et al. 2010). I rather think that trait and function are linked by monotonous functions, but traits are generally not independent and another monotonous trait-function relationship can constrain the first function. For example, the exchange function of the leaf (and photosynthesis activity), is negatively linked to the thickness of the leave (promoting thin leaves for a higher light capture and photosynthetic activity, but the lifespan and mechanical support of the leaf require denser leaves to be viable. This trade-off in functions, linked by a trade-off in traits (the leaf cannot be both thin and light in one hand, and robust and self-supporting in the other), lead to the emergence of a strong constraint ("hard frontier" in figure ??) on one side of the relationship, while competition processes out-select combinations of traits that are not relevant on the other side ("hard frontier" in figure ??).

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. Global characterisation of these constraints should allow a better representation of plant functional diversity.

2.2.2 Strategy-spaces made of trade-offs

Plant diversity is expressed, and visible to anyone, by the variation in shapes and colors, scents and growth forms, but this diversity is the demonstration of the multiplicity of strategies. In an early attempt to make sense of this diversity of strategy Grime (1977) theorise the existence of two type of constraints that shape plant communities: perturbations and stress. The perturbation axis captures the variability of community drivers, while the stress axis captures how conditions facilitate or make difficult plant establishment. They draw a two-dimensional space where three regions can be invaded[1], corresponding to three different strategies: competitive (C) in low stress-low perturbations region, stress tolerant (S) in high stress-low perturbations region, ruderal (R) in low stress-high perturbations region, forming Grime's triangle (*see* fgure 2.5).

Grime's triangle set the basis for strategy space, and the broad meaning of *stress* and *perturbation* terms allow them to be applied to various conditions. However, the diversity of types of stresses (drought, cold, nutrient availability) and perturbations (predation, fire, avalanches etc...) cannot be specifically captured by such wide concepts. Westoby (1998) highlight the difficulty to use such space and its incapacity to explain some patterns. According to him, a strategy space[2] should:

- "express meaningful differences in ecological behaviour between species";

- allows to "position a plant species from anywhere in the world within";

- be composed of attributes that "require little enough effort to estimate";

- lets "possible to quantify the extent to which the [strategy-space] captures variation in other plant attributes".

He proposes to use functional traits to meet these criteria of functional differences, generalisation, and practicality. Three traits capture the components of
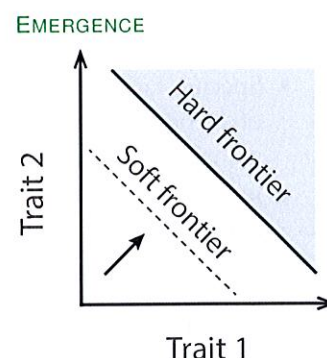
EMERGENCE

Figure 2.4: Emergence of trade-offs between traits because of hard physical-biologivcal frontiers, and "soft frontier" due to selection.

FROM THEORY TO TRAITS

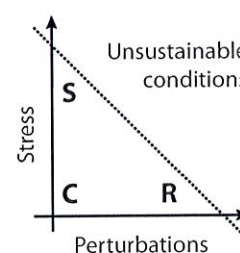[1] high stress and high perturbation regions does not allow establishment

Figure 2.5: Grime's triangle. Competitive (C), stress tolerant (S), and ruderale (R) strategies are dominant in the three regions of the perturbations-stress space.

[2] called Plant Ecology Strategy Scheme (PESS) in his paper

Grime's triangle:

- Specific Leaf Area (denoted L): captures the speed of return of investment of carbon in leaf, as latter highlighted in the LES. High SLA is generally associated with competitive species that capture a lot of light and have a high growth rate. At the other end of the spectrum, low SLA species are more stress tolerant. This axis is the practical equivalent to the axis CS in Grime's triangle.

- Height at maturity(H): the race to the light (but not time fixed as the protocol for functional trait measure encouraged it), but also capture ruderal axis (time interval between perturbations)

- Seed mass (S): expresses the capacity of a species to invade freshly disturbed environments or the competitive advantage seedlings possess with a larger starting carbon pool. This trade-off between the competitive strength of seedlings against the chance of invading freshly disturbed environment capture well the CR axis of Grime's triangle.

The LHS strategy space proposed by Westoby has the advantage to be easily measurable and to allow comparison between species all around the globe (Pierce et al. 2013).

This approach can be further extended with multiple traits. Indeed, global datasets and databases of functional traits reveal global scale correlations between traits. These correlations, or trade-offs, simplify the representation of plant species (Díaz et al. 2016) and translate fundamental axes of strategy differentiation (**reich_world-wilde_2013**). Yet, plant communities exhibit extraordinary species and functional diversity, suggesting that not all traits are correlated. Trade-offs emerge because of hard (physical, chemical or biological) and soft (competitive pressure) constraints on combinations of functional traits (see figure **??** and Shipley et al. 2006). Therefore, for a given couple of traits, the physical independence of traits and the independence of ecological processes they are involved in should ensure the absence of trade-offs between those. While some traits are related to multiple physiological processes (a composite trait like SLA is involved in water regulation, but also light capture and tissue toughness), traits are often specific to one or two processes.

GENERALISATION OF STRATEGY SPACES

These processes must have an ecological significance, so filtering processes are the best candidate to observe such trade-offs. Against climatic filters, plants can either escape (*i.e.* finish a life-cycle before the filtering event) or avoid/resist (develop specific tissues or strategy to pass the filter). This can be observed for drought (Kooyers 2015) or frost (Körner 2003). The resource use strategies and reproductive strategies are also orthogonal (**diaz_global_2014**). From this, a generic principle can be formulated stating that the number of observable trade-offs in an ecosystem is close to the number of constraining processes. It is supported by the observation that a limited number of traits (or dimension, or trade-offs) is often enough to capture the diversity of vegetation community as in Laughlin(2014)

The independence of strategic trade-off justifies that these trade-offs can be used as independent dimensions of a **strategy space**, defining the diversity of strategies present in a community.
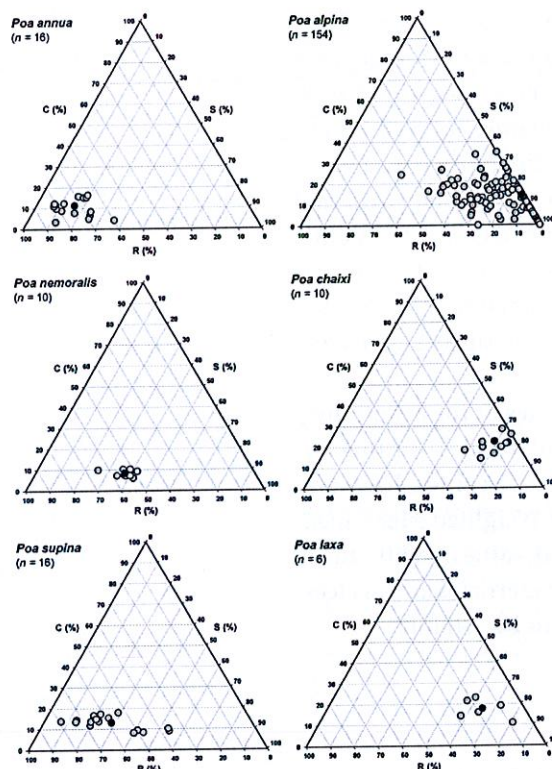
Figure 2.6: Empirical evidence of the CSR triangle in natural communities. The CSR triangle is created by the translation of a multivariate analysis into a coordinate system (see Pierce et al. 2013 SI for details). "CSR classification of six species of the genus Poa from lowland (left column; P. annua, P. nemoralis, P. supina) and alpine (right column; P. alpina, P. chaixi, P. laxa) northern Italy. Grey circles represent the strategies of individuals, and black circles the mean strategy for the species based on the individuals included in the analysis." from Pierce et al. 2013.

The existence of such low dimensional strategy spaces have been observed at large scale (Pierce et al. 2013; Díaz et al. 2016) but also at smaller scales, where the CSR triangle could be identified in ecosystems where precipitation stress and grazing perturbation are shaping the community (Frenette-Dussault et al. 2012).

EMPIRICAL EVIDENCE

unclear sentence

The multiplicity of processes shaping vegetation systems leads to similarly constrained diversity in plant strategies. These strategies are captured in a strategy space *spanned* **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, while parameter set allows easy characterisation of species and communities.**

2.3 How traits link to ecosystem properties

Now that functional traits, trade-offs and strategy spaces are identified as good candidates to characterised the plant functioning and differentiate species, can we link functional traits to **ecosystem properties** and by extension to ecosystem services?

2.3.1 Mass Ratio Hypothesis, Community Weighted Means, and functional identity *(section X.Y)*

drowned earlier

As explained, plant species, based on their identity, provide ecosystem services. Some of these services are direct consequences of the characteristics of the species and their functioning. Because of that, Grime 1998 formulates the **Mass Ratio Hypothesis** that states:

> ... the extent to which a plant species affects ecosystem functions is likely to be closely predictable from its contribution to the total plant biomass. - Grime 1998

[margin note: categorical variables]
[margin note: ? (other continuous)]

Because functional traits are quantitative variables, they can be manipulated more easily than factors. Therefore, while phytosociology describes vegetation communities with broad types and approximate abundances, trait-based ecology benefits from this continuity to characterise mean properties of community. The **Community Weighted Mean** of a functional trait is the average of species-specific trait values weighted by the relative abundance of each species, and corresponds to an extended mathematical application of the mass ratio hypothesis when functional traits are linked to services. These summary variables define the communities in a quantitative way similar to the functional trait for species. In addition to be quantitative, it is functional and responses to disturbing factors can be predicted (Lavorel and Garnier 2002).

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 identity of the species. 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.

2.3.2 Benefits of diversity

Certain processes are determined by the most abundant species of a community, but other services and functions may result from the properties of the group. **Diversity** is the most important property of an ecosystem or a community for a wide audience. This measure is peculiar to groups of organisms and plays a major role in its functioning and the services it provides. Diversity can refer to species richness or functional diversity. The former quantifies the number of species present in a habitat and can take into account the relative abundance of the species. Many indexes can be used to measure this variable representing different perspective or aspect of the metrics (see **chalmandrier_communities_2015** for exhaustive information).

Functional traits and functional diversity can be used to estimate certain ecosystem services. For example, the diversity of phenology captured in flowering periods (see figure 1.2) is an indicator of the recreational function of mountain grasslands.

But diversity also supports indirectly functions and other properties of the system. Multiple mechanisms explain this multiplicity contained in the measure of diversity.

First importance of species richness is found in the insurance effect that prevents the loss of a function or a service with the loss of a species by ensuring that multiple species provide such function or service (see ● species in figure 2.7). Because insurance effect relies on the redundancy of function, this effect is better captured by species richness than functional diversity. Another way of seeing this notion is the selection effect that states that increasing diversity increases the potential number of services provided by the community (see ● species in figure 2.7), as each species added can provide new function/service (or at worst reinforce already present ones). When the function or service is directly linked to a trait value, this selection effect is directly captured by an increase in functional diversity.
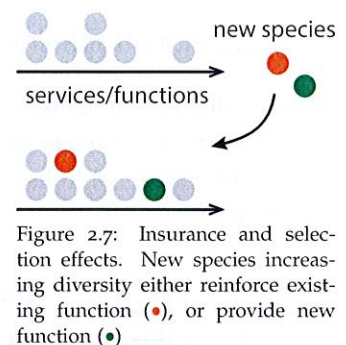
Figure 2.7: Insurance and selection effects. New species increasing diversity either reinforce existing function (●), or provide new function (●)

Functional diversity is also associated with higher productivity and resistance to invasion or perturbation events due to niche complementarity mechanisms. *citation*

Species richness and functional diversity are often strongly correlated, but they do not capture the same services or effect. Functional diversity is a strong indicator of niche complementarity and its benefits.

2.3.3 Productivity: both community property and ecosystem services

Productivity of a plant community is mostly sensitive to abiotic conditions, precipitation, nitrogen, and temperature being the main variables influencing this productivity. Because of that, there is a large contrast between ecosystems in contrasting environmental conditions (tropical forests and mountain grasslands — *give exampls of productivity of ecosystes.* being two extremes). These differences can be observed in the distribution of functional traits of species, size and resource use related traits being the most *telling* eloquent ones.

While community productivity depends heavily on environment properties (climate, soil), it is also dependent on the community, its richness, and the dominant species. The abundance of highly productive species, characterised by high nutrient content, fast-growing and exploitative strategies is responsible for most of a community productivity. Nevertheless, it is hard to disentangle the link between the productivity of the habitat and the productivity of the species living this habitat.

The productivity has another ambiguity: it is both a property of the system and a service. It's a property, and is important in ecosystem services assessment as some services will scale with productivity (*e.g.* carbon storage). But it is also a service, it measures fodder production in grasslands, but wood production in forests, etc... *citation*

Productivity is at the same time a property of the habitat, of the community, *and* and it is a service. While the role of abiotic factors is prominent, the effect of the dominant species and the community structure on productivity should not be ignored.

2.3.4 Trade-offs in ecosystem properties

Traits can be linked to ecosystem services by *a* statistical framework (**lavorel_how_2014**). But, in the same way there are trade-offs between traits, the ecosystem services provided by an ecosystem are also constrained. Understanding these trade-offs and the dynamics of the community dynamics allows to capture *the* these trade-offs between services bundles (Lamarque et al. 2014). This link should encourage ecologist*s* to focus on the development of methods to link drivers of ecosystems to community dynamics, to predict changes in ecosystem services (see figure 1.4 in chapter I).

In addition to facilitate the study of the effect of abiotic conditions and biotic interaction, functional traits can be used to describe the community and its main properties to evaluate ecosystem services. Statistical links that can be used to determine these links, and research effort should better *would probably* focus on the dynamics of grasslands communities and the changes in main properties.

2.4 Modelling diverse plant communities

Modelling mainly consist in deciding what is important considering and worth representing. The choice of how an entity or a mechanism is represented also correspond this decision making. While considering vegetation community the choice can be on the resources needed, the type of perturbation, or the part of the life cycle of most importance. For vegetation models for the study of community properties and dynamics, the representation of the interactions of multiple species is key. The strategy-space concept offers a great solution to both the interactions and the diversity of species, while also informing the modellers of the communities' properties.

2.4.1 How strategy spaces open vegetation modelling

In a mechanistic model with multiple species, strategy-spaces are simplified ways to define multiple species. Species identity is fully defined by its position in this space of species-specific parameters. This is a great advantage compared to traditional approaches of vegetation models that rely on strong knowledge of represented species. Because mechanistic models function with shared biological and ecological processes, the differences of behaviours between species emerge not from the functions but from the species-specific parameters. Therefore, to properly model a species behaviour, in addition to having properly modelled the processes, all species-specific parameters for all species must be determined. This step requires a large investment of time and resources and is proportional to the number of species. Strategy space based on trade-offs enable the representation of multiple species, in a closed environment. A greater effort is required to establish such strategy space, as it needs identification of strong trade-offs and the delimitation of ranges along the axes of strategic differentiation. But once established, an infinity of species can populate this robust space without the threat of Darwinian demons. This subject is further discussed in the following chapter (chapter III, section 2). Because of that strategy space are great tools to consider a diversity of species, when the identity of species is not of primary interest.

While I have no knowledge of living species being projected on a strategy space used in a simulation model, it can be imagined with a projection of measured traits on traits used in the model (even if there can be some discrepancies between the two spaces), in the way of Pierce et al. 2013.

Dynamics Global Vegetation Models tend to use such strategy spaces to model high diversity with a limited number of traits. These models, mainly represented by the model of Kleidon and Mooney 2000, and extensions Reu et al. 2011; Pavlick et al. 2013. They use 12 to 15 traits in their strategy space. These traits can be grouped in: allocation traits, tolerance to climatic conditions, resource efficiency, reproduction strategy and tissue turn-over. All these traits are linked to trade-offs in the formulation of the model. A general observation we can make is that these trade-offs often take the form of greater growth or efficiency against greater resistance to stress. This is similar to observed strategies in drought environments(Kooyers 2015). These models (Reu et al. 2011; Pavlick et al. 2013) demonstrate the ability to capture diversity and climatic response patterns, better than plant functional types, with a limited number of traits.

THE POSITION MAKES THE SPECIES

unclear

IN DGVMs