

II

BACKGROUND: COMMUNITY DYNAMICS, TRAITS AND PHENOTYPIC PLASTICITY

① based on a
This chapter is dedicated to the review of the literature and aims to introduce the concepts and hypotheses used and interrogated in following chapters. A link between properties of the community and the ecosystem services is first drawn, then I examine the use of functional traits to represent plants, plant functioning, and communities. Finally, the impact of intra-specific variability, in particular phenotypic plasticity, on community properties is interrogated. *not a common english word*

While this thesis is a modelling thesis, it is not a modelling textbook, and rather than an exhaustive description of the different types of models the focus will be given to selected modelling examples close to the context of this work.

placed on

1 UNDERSTANDING COMMUNITY DYNAMICS AND PROPERTIES: DRIVERS AND THEORIES

1.1 Community assembly and coexistence

1.1.1 Filtering processes: from potential to realised niche

A community is defined by the ensemble of species that coexist within the same space and time intervals. Communities were first viewed as a group of species that have evolved together to survive within specific conditions. To maintain itself within the community, each species needs to grow during the vegetative phase, survive and reproduce. These steps of the life cycle result from the coordination of multiple physiological processes, supported by the extraction and use of essential resources: light, water, and nutrients. A part of community ecology sees communities as discrete entities with specific characteristics. This view is particularly practical for management as the community type can be associated with certain properties and services, or even particular dynamics and management systems. This view is the base of phytosociology as it is still used. While a discrete approach to community ecology provides practical categorisation, it ignores the fundamental dynamic nature of living systems. In a context of global changes, considering the dynamics of plant communities is crucial to predict how these systems will react to conditions never experienced. Another approach to community ecology considers that communities emerge from the distribution of individuals of a species, *the* distribution controlled by its genetic and physiologic characteristics and its interactions with other species (Gleason 1926, Whittaker 1975). The distribution of individuals depends on how it is affected by abiotic conditions and interactions with other species or biotic conditions. The joint effects of the abiotic and biotic environment are captured by the concept of niche (elton 1927). The niche of a species is defined by how a species population reacts to abiotic and biotic conditions (resource, competition, predation, survival) and how it impacts its environment. Defining the niche of a species is primarily defining the barriers that constrain the distribution of the individuals of the species.

PLANT COMMUNITY

Literature

*but are several
with overlap
realized, potential)
→ Hutchinson, H*

The **abiotic filtering** designates the non-biological variables that prevent the establishment of a species in a habitat. This term generally refers to climatic conditions and resource availability because temperature, water, nutrient and light availability are the main variables that constrain the plant development. Other abiotic factors can be considered, such as salinity (L. Poorter and Bongers 2006) or soil properties (pH). These variables determine if a plant (depending on its specific properties) can establish in a given habitat without any biotic interactions. These filters define, for a given habitat, the pool of species (or individuals if genetic variations are considered) that can grow and reproduce in this habitat without interaction. The ensemble of habitats a species can invade if only the abiotic factors are considered is called the **potential niche** (see figure 1.1). *fundamental?*

ABIOTIC FILTERING

In addition to this large scale filters, another barrier may prevent a species to invade a habitat: its access. Indeed, dispersion plays a major role in the geographical extent of a distribution area of a species. Dispersion barriers such as mountains, seas or ocean prevent uniformisation of vegetation and reduction of global diversity. Such limits explain the existence of endemic species that grow only in a few locations, despite a larger potential distribution area (*of* defined by potential niche).

DISPERSION FILTERING

Finally, the main factor that can affect the ability of a plant species to establish, is living interactions. For plant species, herbivory and competition are the most important factors, but other forms of interaction can affect the potential niche. The resulting niche, after all filtering processes, is called the **realised niche**. Competition affects the growth of the focal plant indirectly by reducing the availability of resources, increasing the stress of the plant and reducing its niche (see the interaction between species 1 and 3 in figure 1.1). Competition interactions are major factors shaping vegetation community and are extensively studied both with theoretical (Chesson 2000a; Amarasekare 2003) and empirical approaches (Kunstler et al. 2016).

Similarly facilitation interactions also affect indirectly the levels of resources experienced by the focal plant, but in a way that is positive for the focal plant. So they widen the realised niche outside the potential niche (see the interaction between species 1 and 3 in figure 1.1). There are hypothesised to be larger along a stress gradient, where competition interactions are filtered out because they do not allow species maintenance and only positive interactions remain. Such relationships are dependent on the pair of species considered and may change depending on conditions (Callaway, Pennings, and Richards 2003).

From the point of view of the focal plant, these interactions only exist through the changes in resource availability (even if plants are able to identify their neighbours). In this sense, we can see potential and realised niches as displacements of the fundamental niche (niche defined in term of experienced conditions, stresses and resources) within spaces defined by abiotic variables or biotic variables. From this framework, the fundamental niche, or conditions experienced by the focal plant, is the stronger representation of the species niche and the realised niche (abiotic and biotic filters on the niche) emerge from the effects of external factors on this experienced environment.

This point of view should be adopted in models (Berger et al. 2008) because it allows the representation of both abiotic and biotic factors in a shared and generic framework. This is an improvement in comparison to models requiring

BIOTIC FILTERING

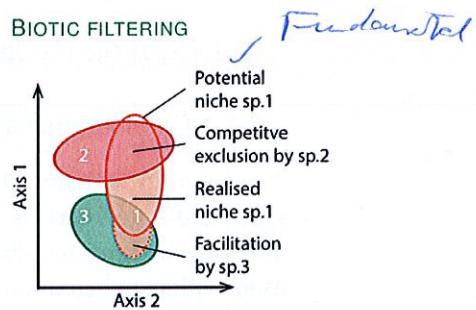


Figure 1.1: The potential niche of the **focal** species is reduced by competition interaction with **species 2**, but extended by facilitation interaction with **species 3**. This representation of the niche requires the knowledge of the effects of both abiotic factors and all pairwise interactions with other species. A more mechanistic approach of the niche should be considered in IMBs. *IBMs? can?*

FUNDAMENTAL NICHE

unclear what is the relationship between potential and fundamental niche. can you visualise it in Fig. 1.1?

a matrix of interaction coefficient between species. Such matrix, in addition to being hard to parametrise, cannot be used in a framework of dynamic strategies. Modelling effort should instead be on explicit temporal and spatial dynamics of resource dynamics. Plant interactions would be captured by the effects of plant functioning (reduction of resource levels in relation to plant growth and resource use) on these dynamics (Berger et al. 2008; Morin and Thuiller 2009). → why?

The concept of ecological niche serves as a great tool for theoretical research on coexistence. It encompasses in a convenient way both abiotic and biotic filters of one species distribution. While traditional view of the niche requires considering both abiotic filters and pairwise interaction, fundamental niches and resource dynamics modelling offer an alternative to model realised niches as an emergent property of the model.

1.1.2 The complexity of coexistence

If one want to better understand and predict dynamics of complex systems, they first need to understand how such complex system is assembled. Niches can be used to characterise a range of habitats a plant can live in, but because of complex inter-specific interactions, determining the final composition of a community from the list of species that can live in this habitat is not easy. If it is easy to observe diverse ecosystems (from bacteria to plants, insects or algae), it is challenging to determine the processes that 1) group the entities together (in time and space), 2) maintain an apparent stability in the group composition (at least at a certain spatial and temporal scale). We can imagine biotic filtering as a physical filter, the same way the abiotic filter is often illustrated, but this image does not translate the dynamic and complex nature of underlying processes. Biotic filtering emerges as the result of all the interactions between the entities that make it through the other filters. And how these interactions, direct or indirect, play together determines the stability of the diversity.

THE QUESTION OF COEXISTENCE

citation,

To predict the outcome of competition interactions, multiple theories have been developed. Among these theories, we can cite two that have a different perspective on the same question: how do species sharing essential resources coexist in a homogeneous environment?

Chesson (2000) tends to have a population dynamic view of the system and identifies two types of processes that promote coexistence: (1) stabilizing mechanisms, (2) equalizing mechanisms. The former are required to stable coexistence as it a condition of invasibility. In other words, plants can coexist only if one species can invade the other. The condition to such invasion is that the species at low-density growth better than the species at high density. This is the case if intra-specific competition is higher than the inter-specific competition. Equalizing mechanisms are processes that diminish the fitness differences between the species, without ensuring stable coexistence. This framework is extended by Adler, HilleRisLambers, and Levine 2007 in the modern coexistence theory. It states that niche differences (Levine and HilleRisLambers 2009) and fitness differences are the two mains axis of species coexistence. They make the assumption that niche differences define the relative strength of inter-specific versus intra-specific competition. The larger the differences between niches, the thinner is the overlap, and the weaker the inter-specific interactions. Therefore,

this can be related to stabilizing mechanisms in Chesson (2000a). On the other end, fitness differences also impact coexistence. The lower the differences, larger are the chances species coexist. The importance of niche differences required for stable coexistence decreases with the decrease in fitness differences.

In the other hand, Tilman elaborates a theory (D. Tilman 1982; D. Tilman 1988) around resource use more in line with the idea of fundamental niche expressed in the previous paragraph, the contemporary niche theory. Species are characterised by the impact they have on the resource, and they use the resource for growth. Competition is in favour of the species with the lowest requirement for the resource because competition leads to resource deprivation it can survive. But coexistence if there is more than one limiting resource. In this case, coexistence can be achieved if species have a stronger impact on the resource from which they benefit the most (and intersecting zero net growth isolines).

These two theories give strong conditions for stable coexistence; however, they required simplifying hypotheses (all other things being equal, homogeneous environment) that are not met in natural environments. Despite their different approaches, these theories can be united as demonstrated by Letten, Ke, and Fukami (2017) if the impact and benefit coefficients from contemporary niche theory are translated into niche and fitness differences. Despite this unified theory, they applied to a too limited range of situations to be applicable in the context of diverse mountain grasslands.

Plant community requires strong coexistence mechanisms to maintain species richness. Single theories fail to predict high diversity observed in plant communities such as natural mountain grasslands. However, high dimension coexistence processes and complexity seem to be an answer to the biodiversity paradox. In addition to niche based coexistence processes, other mechanisms that promote coexistence must be considered.

1.1.3 Variability and dynamics: driven by the resource

Resource dynamics, even with constant influxes, seems to be the key to understanding plant interactions and dynamics according to Tilman (D. Tilman 1988). Can the resource distribution in time and space explain coexistence?

In Tilman's perspective, resources are driven by two things, external influx and internal (to the system) consumption or cycle. The system's structure and composition is responsible for resource dynamics as much as external influx. And these dynamics alter the structure of the community and change the hierarchy within the community. This cycle is well illustrated by the cycles we can observe in forest systems and gap models. Mature forests produce big openings that fall down and create perturbation within the system. The resulting hole in the canopy allows for pioneer species to invade this space without competition. While they grow, other slower species are in shadows and must tolerate this competition, and grow enough to out-compete first established species. Because there is a trade-off between potential growth and shade tolerance allowing this cycle to set up, there is a succession dynamic after each perturbation of the systems. These local events of perturbation support coexistence at a large scale, a coexistence that can be captured by spatially explicit models (Jérôme Chave 1999; Falster et al. 2016)

COMMUNITY DYNAMICS

→ typical would be
Letten et al. (2017)
} unclear
do they? } this section
is not sufficiently
well argued.

Such drastic dynamics do not exist in mountain grasslands' communities. But the natural temporal variability of resources due to contrasted seasons also drives diversity in growth strategies. Coexistence comes to the existence of multiple climatic contexts at the same place (but not the same time). As plants cannot be the most competitive species for any given condition^{all} in the whole range of conditions experienced in mountain habitats, there is a succession of species at the top of competition hierarchy (Adler, HilleRisLambers, Kyriakidis, et al. 2006) (see figure 2.6 for illustration). The diversity of flowering periods in figure 1.2 is an evidence of this succession dynamics.

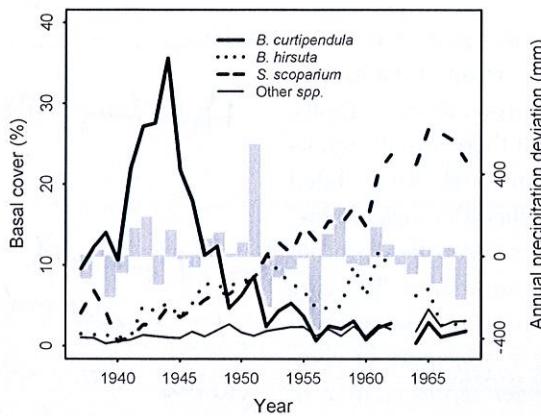


Figure 1.3: Changes in observed basal cover for 3 grassland species. This variation in hierarchy illustrates the succession in grassland communities and the storage effect due to the stabilizing effect of climatic variation promoting coexistence. See details in original study by Adler, HilleRisLambers, Kyriakidis, et al. 2006.

This mechanism promoting coexistence because of succession dominance driven by temporal changes in environmental condition is called storage effect. The species grow when the conditions match their niche and store the gains to wait until next favourable conditions. This term is generally applied to yearly variations, but the idea can be applied for variations within a growing season, allowing growth and storage until next season.

The temporal variations have a stabilizing effect on coexistence G. D. Tilman 1984, but maybe more intuitively, spatial heterogeneity also promotes coexistence. Indeed, spatial variations of conditions at small scale create multiple niches that allow for diversity if measured at a higher scale. This spatial heterogeneity can be overlooked, but in the context of mountain grasslands, where plants are generally small due to high-stress levels and a very fine scale heterogeneity resulting from the terrain texture, it can play as a strong stabilizing mechanism.

Spatial and temporal heterogeneity play a major role in coexistence maintenance by creating various opportunity^s or niches, in a given ecosystem. Internal dynamic variation of conditions also support stable coexistence.

1.2 The complexity of diversity

While resource use strategies and resource heterogeneity are important mechanisms for diversity, dispersal processes and meta-community dynamics should also be considered. Grassland communities are not independent of one another, but they are connected by dispersal vectors such as wind and animals. These connections support diversity but not stable coexistence, but remains crucial for community dynamics. Indeed, the link between the community and the meta-community (all connected communities) is a source^s of species that can be absent many

TEMPORAL HETEROGENEITY

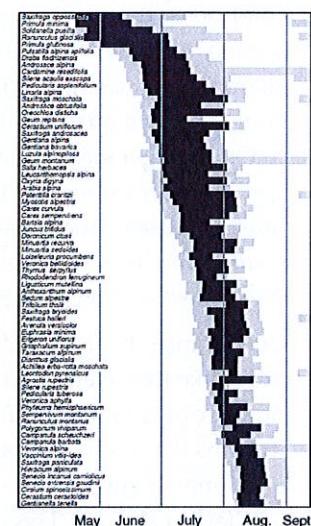


Figure 1.2: Diversity of flowering periods of alpine species. Evidence of succession in grassland ecosystems. From Körner 2003.

SPATIAL HETEROGENEITY

LARGER SCALES DYNAMICS

from the focal community. Therefore, in case of transition of environmental conditions, these external species can invade the focal community, accelerating species turn-over compared to a closed community. In the context of global change, it is essential to consider mountain grasslands communities as open systems as the question of invasion by lower altitude species is yet to be solved.

Other larger scale dynamics can impact community dynamics such as species-specific interactions (herbivory or ~~polinisation~~) that lead to dynamic equilibriums. However, modelling such processes are demanding, and while it maintains some diversity, it is not expected to be the main driver of grassland dynamics in the context of global change.

Coexistence theory has difficulties explaining high species diversity in communities like freshwater diatoms or mountain grasslands that compete for a limited number of resources in fairly stable conditions. From the previous paragraphs, it seems that these environments are not that stable and that there are numerous mechanisms supporting diversity. Diversity is highly dimensional as it is stated by Clark et al. (2007). This complexity, that we just have scratched the surface here, is too high for theoretical models to handle. That does not mean they are not useful, but they cannot consider all these processes at the same time. To study diverse communities, it is required to incorporate at least parts of this diversity in mechanistic models. While it increases the modelling work, model's complexity, and difficulty to analyse results, it allows a stronger representation of communities, of their diversity and enables the identification of main processes, and possible interactions:compensations:synergies between these processes.

The evaluation of services relies on a good representation of the plant community and its essential properties. To represent complex interacting systems like vegetation communities, descriptive approaches and theoretical models are not sufficient. The main driving processes must be considered and explicitly modelled. Explicit heterogeneity and dynamics of the resources are key to understand and model filtering processes, coexistence mechanisms, and community dynamics. Modelling both community properties and resource dynamics require an understanding of plant functioning and diverse growth strategies. The challenge of community modelling is not to keep simplicity in its structure, but increase diversity in its processes.

→ I don't think it a good strategy to argue in the sense that your model approach is the right one.
Focus on how it complements

2 HOW TO REPRESENT PLANT COMMUNITY

All plants share the same pool of essential resources and similar physiological processes of assimilation and allocation, however, species differ by their growth rates, niches, and competitive abilities. How do such differences emerge from a common functioning wireframe? It seems that these differences can be explained by differences in parameters that characterise this functioning. So considering this diversity is required to represent the diversity observed in mountain grasslands.

What happens
you make sweeping statements
here without any backing,
and avoid,

EMBRACING COMPLEXITY

Are they there?

→ I would say that it is interesting to study whether we can create similar levels of diversity "in silico" as found in nature with a more realistic level of processes as found in theoretical models.

} well, making things more complex is easy...

A

The challenge of modern community ecology is to determine the trajectories the existing ecosystems will follow under new environmental conditions. Species centred approaches, because they are limited to the knowledge of existing response patterns to existing gradients, cannot tackle this problem. How can a new representation of plants enable generalisation of the diversity of plant functioning in new conditions?

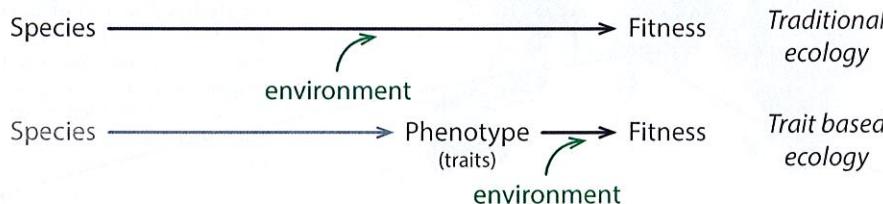
Jully

2.1 The continuity of functional ecology

2.1.1 Shift in paradigm: traits and patterns

Classical use of niche theory can be observed in Species Distribution Models (SDMs) that link the probability of presence of one species to a multidimensional description of a habitat. The environmental variables are literally used as the dimensions of the Hutchinsonian niche, and directly link the species to its fitness in a given environment (see figure 2.2, first row). This method is widely used to model environmental niche¹, but some can also include species interactions to incorporate an explicitly biotic filter. SMDs have good theoretical support and have a lot of practical applications, however, their strength is reduced at the scale of the community where the biotic filtering processes and fine scales dynamics take the advantage over large-scale abiotic filtering. Also, because they require a lot of data for any given species, they lack generalisation properties to be applied to rich communities. Community dynamics require fine-scale plant functioning processes to capture the effects of small scales variability and plant interactions, drivers of coexistence.

This example of modelling approach based on a species centred framework reveals the weaknesses of this framework. The distribution of a species along gradients, or its niche, while it can be captured by abiotic variables, is primarily determined by the fitness components (and whether or not they lead to a positive fitness): growth, survival, reproduction. These variables are not intrinsic properties of species but emerge from the interaction between physiological processes (carbon assimilation by photosynthesis, water absorption, organic matter allocation, etc...) and the environmental conditions. Only considering these processes allow to explicit and decompose plant functioning, and therefore model it in new combinations of environmental conditions.



Most of plant species share the same growth, survival and reproduction processes, but they still differ in these aspects as a function of the abiotic and biotic environment. The solution to shift from species centred paradigm, and its couple habitats-species (or species-environment-abundance like in SDMs), is to explicit the phenotype of these species. By using functional traits to define the

Again rather
than saying anything
cannot be done,
point out difficulties
and propose a
alternative (that comes
with its own problems)

→ diversity of questions → diversity of models
A SHIFT NEEDED

presence → the
relationship between
presence and fitness
is not trivial

disruptive → the
type of data they
require is more and
more available.
But they do not
represent transitory
dynamics

Figure 2.1: The shift toward trait-based ecology allows for the decomposition of the link between species and fitness determined by the environment. On one hand, the link between species and traits is better characterised by standardised protocols and the use of databases such as TRY (TRY). On the other hand, the link between phenotypes (defined by trait values) and fitness can be generalised and the role of environment in this relationship better understood.

phenotype of a species, ecologist can limit the representation effort to the link between traits and fitness physiological properties (P. B. Reich, Walters, and Ellsworth 1992), and then link species to traits with simpler data collection procedure (Cornelissen et al. 2003) (see figure 2.2, second row).

This shift in paradigm allows for a simpler and functional representation of plant species, that can be later linked to physiological or ecological processes.

The functional traits allow the decomposition of the link between species and fitness, to gain general understanding instead of specific relationships between species, environment, and fitness. However, this decomposition also breaks down the species, that can no more be described by one word, but needs instead multiple quantitative values to be described. ~~To~~^{the} singularity of the species is exchanged ~~the~~^{for} the multiplicity of traits. The link between species and fitness, now broken down by traits, can be analysed in a new light, parts by parts.

This decomposition allows the identification of relationships between morphological traits (easy to measure) and physiological traits (more interesting but harder to measure) (D. D. Ackerly and Peter B. Reich 1999; L. Poorter and Bongers 2006; Peter B. Reich 2014). Response patterns along climatic gradients have also been identified (Niinemets 2001) increasing the understanding of the role of the functional traits for the performance of plant species.

This trait-based approach, demanding in data collection effort, benefit from the consistency of the measures (Cornelissen et al. 2003) allowing pooling of the data into big databases such as TRY or Glopnet. The standardised collection of data all around the globe is a model of centralisation and collection that can lead to major large-scale pattern enhancing the understanding of the functioning of plant communities.

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THE RISE OF FUNCTIONAL TRAITS

citation

ARE THERE PATTERNS?

hot memory
for what
kind of
study
Careful



Figure 2.2: Distribution of the sample locations around the globe. The full set of data compiled from 121 studies consisted of 39 needle-leaved and 558 broad-leaved C₃ and C₄ trees and shrubs from 182 geographical locations. Example of large dataset compiled from widely distributed sites. From Niinemets 2001.

But the functional traits can be used at a more local scale to disentangle the species and the community responses Kichenin et al. 2013; Jung, Cécile H. Albert, et al. 2014.

The complexity of coexistence and community dynamics processes could not be captured with traditional species centred ecology. The last two decades

saw the rise of functional ecology and its ability to capture quantitatively the relationship between vegetation and abiotic gradients. The capacity to generalise ecological patterns thanks to easily measurable traits open the door for generalised theories on the plant functioning.

2.1.2 Traits and competition

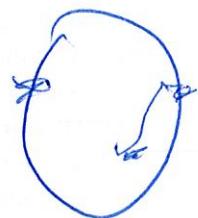
Jayshree

If traits can describe a species and capture its functioning, it is logical to consider them to assess competitive interactions. Two visions have been developed to capture relative interactions. As mentioned in paragraph 1.1.2, trait distance can be a measure of competitive strength. This interpretation is an extension of the hypothesis of the limiting similarity that states that two species with similar niches cannot coexist. If plant functional traits can be used to define the niche, then, trait dissimilarity should be a measure of competitive interaction: the greater the dissimilarity, the lower the interaction. Because the competition is proportional to the absolute distance between traits, the relationship between distance and competition strength is symmetrical. On the other hand, some argue that competition interactions are not all symmetrical, but hierarchical, and that some traits can capture the competition sensitivity and others the competition impact (Kunstler et al. 2016), therefore the intensity of the competitive interaction is not symmetrical and dependent on the relative trait difference, but rather on the relative strength of impact traits compared to sensitivity traits. It seems that the form of the relationship depends on the type of competition mechanism considered. It will be hierarchical if they compete for the exact same resource (light, water), and symmetrical otherwise (temperature resistance, specific predation avoidance, pollinator, etc...).

Understanding how competition (or any other interaction) is regulated by traits is important to determine competition outcomes with alternative methods than pairwise coefficients that require empirical data to determine. Linking traits and strength of competition interaction would also allow the intra-specific variations to be considered. In this case, determining the exact relationship between trait distance and the competitive effect is crucial as it would change the effect of intra-specific variability (see Hart, Schreiber, and Levine 2016 for example).

But these interactions are not only symmetrical or asymmetrical, there can be non-transitivity promoting dynamic stable coexistence (Levine, Bascompte, et al. 2017), or be context dependent (Callaway, Brooker, et al. 2002). Moreover, the nature of the competition relationship (dissimilarity or hierarchy) depends on traits considered (Bennett et al. 2016). Due to their complexity, interactions cannot be summarised by single trait value comparison but is multi-dimensional (Kraft, Godoy, and Levine 2015). However, traits can inform competitive interaction by informing the plant functioning and the use and effects on the resource.

Traits can be a good proxy for competitive interaction but the relationship between trait differences and competition intensity depends on the competition process. If the interaction is transitive, a strong asymmetric pattern can be observed between interaction effects and trait differences, while symmetric interaction reveals niche differentiation processes. Despite these observed relationships, the specificity and multiplicity of trait-mediated interactions promote the use of mechanistic solutions to capture the multi-dimensional and context-dependent nature of plant interactions.



POTSAT

↳ good, but not explicit enough.

The paradigm shift toward functional ecology allowed the shift from discrete to a continuous representation of species. This change makes easier the representation and study of plant communities, especially along environmental conditions or management gradient¹. Traits are also used to study plant interactions. Trait approaches offer a functional link between morphology and physiology that has great potential in generalising environmental effect² on the phenotype-fitness relationship. However, the need for multiple traits to capture plant niche differences or similar response patterns of multiple traits suggests underlying structure within trait assemblage³. Understanding this structure and how it relates to community dynamics external drivers is crucial in the representation of diverse communities.

Incomplete sentence

2.2 How trade-offs make strategy space

2.2.1 Trade-offs: capture constraints on species differences

The functional link that is observed between some morphological traits and physiological traits suggests underlying processes that link these traits together. It appears that multiple traits are correlated together at the global scale between species (P. B. Reich, I. J. Wright, et al. 2003; Ian J. Wright, Peter B. Reich, et al. 2004; Jerome Chave et al. 2009; Peter B. Reich 2014) and within species (Hu et al. 2015). This correlation between functional traits of the leaf was described at a global scale by Ian J. Wright, Peter B. Reich, et al. 2004. The Leaf Economic Spectrum (LES), defined by these correlations between multiple traits, draws a continuum of strategies. It spreads from species with high resource acquisition rates and rapid growth rates but low tissue lifespan, to species with longer tissue lifespan but lower growth rates. This is a clear description of a trade-off between strategies, opposing exploitative strategies (high Specific Leaf Area (SLA), high Leaf Nitrogen Content (LNC) and low Leaf LifeSpan (LLS)) to conservative strategies.

This axis of differentiation allows ecologists to link quantitative measures to types of strategies that better capture diversity of strategies than discrete typology. These strategies are translated into traits, traits that can be translated into physiological processes parameters, then into components of fitness.

In addition to a quantitative measure of species-strategies, such trade-offs simplify a lot trait-based approaches. While many variables can be measured on one individual, correlations between these variables reduce the number of dimensions to consider. This simplification cannot be better illustrated by the work of Diaz et al. 2004 that demonstrate the existence of two major axes of "evolutionary specialisation" that explain most (41%) of trait variability: size-related traits, and resource use speed traits. Similar evidence is also found on a global scale in addition to evidence for high levels of coordination between axis (Díaz et al. 2016).

Similar correlations could be found in roots (Ryser 1996; Peter B. Reich 2014) but patterns are generally weaker, certainly because of more fragmented data and interactions with micro-organisms that alter the link between morphology and function of roots.

LEAF ECONOMIC SPECTRUM

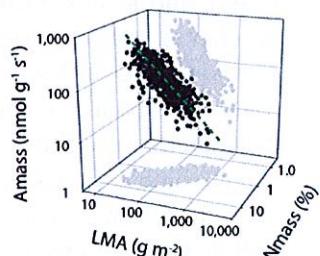


Figure 2.3: Three dimensions of the LES. Correlation of Leaf Mass Area, assimilation rate per mass unit and nitrogen concentration. This correlation reduces three dimensions (more dimensions not shown) into one axis (- -).

STRATEGIES

part my