MASTER THESIS

Niche and fitness differences across environmental conditions and ecosystem types

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Abstract

While the effects of species ecology and environmental limiting factors (ELF) on competitive interactions are relatively well-studied, the nature of the relationship between multiple ELF and species ecology is less well-understood. Here, we seek to identify the combined effects of multiple ELF and species ecology on community niche and fitness differences (NFD), which is dictated by competitive interactions, using both experimental and literature-based approaches.

First, we experimentally identified how combined gradients of two ELF affect community composition, compared to their individual effects. We performed competitive experiments using communities of two phytoplankton sub-species. We described their competitive dynamics using two definitions of niche difference (ND) and fitness difference (FD). Second, using data from literature making use of any mathematical definition of NFD, we compared the type of ecological interactions of four biological systems and their respective determinants of coexistence (ND and/or FD). We computed three general definitions of NFD for pair-wise communities.

Our experiment demonstrated that combined gradients of ELF interact in a complex, unpredictable fashion. However, when increasing both ELF caused an increase of ND and increased equivalence of FD, promoting coexistence. Analysing communities from literature showed that different biological systems contain different types of ecological interactions. ND was generally higher in coexisting communities and was the most common determinant of coexistence, while the importance of FD was system- and definition-dependent.

Complex interactions of combined ELF gradients promote biodiversity, and the specific ecology of the species studied influences the effect of the combined gradients. Different biological systems, with different ranges of biological interactions, will therefore react differently to ELF gradients. Combined effects of ELF need to be considered alongside system-specific biological interactions, in order to accurately forecast the outcome of competition under environmental change. All results showed a qualitative difference based on the definition used, stressing the need of a general and approved framework to forecast and understand competitive interactions.

Résumé

Bien que les effets de l'écologie des espèces et des facteurs limitant environnementaux (ELF) sur les interactions competitives soient relativement bien étudiés, la nature de la relation entre de mutltiples ELF et l'écologie des espèces est moins bien comprise. Ici, nous cherchons à déterminer les effets combinés de multiples ELF et de l'écologie des espèces sur la niche et fitness difference (NFD) de la communauté, à l'aide d'une approche expérimentales et d'une revue de la littérature.

Premièrement, nous avons identifié expérimentalement comment les gradients combinés de deux ELF influent sur la composition de la communauté, comparativement à leurs effets individuels. Nous avons mené des expériences compétitives en utilisant des communautés de deux sous-espèces de phytoplancton. Nous avons décrit leur dynamique competitives en utilisant deux définitions de NFD. Deuxièmement, à l'aide de données tirées de la littérature utilisant une des définitions mathématiques actuelles de NFD, nous avons comparé le type d'interactions écologiques de quatre systèmes biologiques et leurs déterminants respectifs de la coexistence (ND et/ou FD). Nous avons calculé trois définitions de NFD pour des communautés contenant deux populations.

Notre expérience a démontré que les gradients combinés d'ELF interagissent de façon complexe et imprévisible. Cependant, l'augmentation des ELF a entraîné une augmentation de ND et une équivalence de FD, favorisant la coexistence. L'analyse des communautés à partir de la littérature a montré que différents systèmes biologiques contiennent différents types d'interactions écologiques. Le ND était généralement plus élevé dans les communautés coexistantes et était le déterminant le plus commun de la coexistence, tandis que l'importance du FD dépendait du système et de la définition.

Les interactions complexes des gradients ELF combinés favorisent la biodiversité, et l'écologie spécifique des espèces étudiées influence l'effet des gradients combinés. Différents systèmes biologiques, avec différentes gammes d'interactions ecologique, réagiront donc différemment aux gradients ELF. Les effets combinés des ELF doivent être pris en compte parallèlement aux interactions ecologique propres au système, afin de prévoir le résultat de la competition dans le contexte des changements environnementaux. Tous les résultats ont montré une différence qualitative fondée sur la définition utilisée, soulignant la nécessité d'un cadre général et approuvé pour prévoir et comprendre les interactions competitives.

Declaration of Authorship

I, Lisa BUCHE, declare that this thesis titled, "Niche and fitness differences across environmental conditions and ecosystem types" and the work presented in it are my own. I confirm that:

- This work was done wholly or mainly while in candidature for a research degree at the Catholic University of Louvain-La-Neuve and Namur University.
- Where I have consulted the published work of others, this is always clearly attributed.
- Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work.
- I have acknowledged all main sources of help.

The 6^{th} of January, 2020

Contents

Chapter 1

Niche and fitness differences across environmental conditions and ecosystem types

Darwin (1859) was the first to report the potential mechanisms and limits that drive species persistence, which the wondrous biodiversity of our planet depends on. His chapter, *Struggle for Existence*, describes the fight of each species to survive. This struggle has four distinct drivers: the resources on which organisms depend to survive; the environmental conditions that the organism can tolerate; the inter-guild[1] interactions; and the intra-guild interactions. For example, plant persistence is based on, for example, : light ; the soil conditions; competition between plant individuals for seed space and interaction with other guilds for seed dispersal.

The persistence of species relies on the resource availability, the environment and the interactions within the ecosystem. Darwin's reflections led the way toward two developments: the competitive exclusion principle and niche theory which, once combined, gave birth to modern coexistence theory.

Competitive exclusion principle

Grinnell (1904) early work focused on the role of limiting resources in a constant environment, expanding the importance of resource competition. Following this, Gause (1934) opened the discussion of the necessary heterogeneity among the geographical space in order to have coexisting species at a given location. Without enough heterogeneity in the environment, two species competing for one limiting resource cannot coexist (Grinnell, 1904;

[1] Guild is a term that commonly means species having overlapping resource requirements (Chesson, 2000)

Gause, 1934). Indeed, resources limit population growth rate of competing species. Such resources are considered as limiting and include, for instance, resource uptake ability, the consumption rate of the species, and the consequences of resource uptake on available resource concentration (Wedin and Tilman, 1993). Inspired by the work of Gause (1934), Hardin (1960) stated the competitive exclusion principle: two species with identical limiting resources cannot coexist. Thus, the number of coexisting species can be at most equal to the number of limiting factors (Gause, 1934; Hardin, 1960; Levin, 1970). Tilman (1982) cemented the concept by developing the mathematical framework of R^* which translates the lowest quantity of a limiting resource on which a species is able to survive. A species able to reduce the most the concentration of the limiting resource while maintaining a positive population growth rate is the dominant species and has a low R^*. The principle of R^* may be seen as the translation of the species requirement in regards to the limiting resources. The species with the lowest R^* will exclude all other species (Tilman, 1982; Wedin and Tilman, 1993). Tilman (1982) has thus quantified the principle of competitive exclusion from Hardin (1960). His framework served as an example to widen the competitive exclusion principle to more complex interactions. First, the inclusion of species affected by a common natural enemy, i.e. apparent competition (Holt, 1984). In this case, the species that maintains a positive growth rate under the highest consumer density will exclude the other (Chesson, 2000; Johnson and Bronstein, 2019). Moreover, competitive exclusion has also been expanded to include mutualism theory: “Complete competitors for mutualism commodities cannot coexist “ (Johnson and Bronstein, 2019). The limiting resources considers the beneficial exchange(s)/service(s) provide by the interactions (Johnson and Bronstein, 2019).

Niche theory

Grinnell (1924) influenced once again by Darwin’s work, developed the concept of a "niche". He defines it as the abiotic and biotic factors that explain the presence of a species at a given place. A niche is thus the result of the differences between habitat preferences and behavioural adaptations of two co-occurring species (Bartomeus and Godoy, 2018). Hutchinson (1957) took the definition one step further by suggesting a general definition: "the niche of a species is a multidimensional hypervolume, each dimension representing a relevant environmental factor (e.g., temperature, precipitation, etc.)".

Thanks to Hutchinson (1957), the definition evolved from a niche in relation with the environment toward a niche specific to the species (Pocheville, 2015). This revolution enabled MacArthur (1958) to begin the discussion of niche overlap importance in the determination of community composition (Mayfield and Levine, 2010).

Coexistence theory

In the early days of the twenty-first century, Chesson (2000) was the first to unite the principles of competitive exclusion and niche overlap in light of coexistence theory. Since then, the field of coexistence theory has taken great steps towards understanding the maintenance of stable coexistence (Bartomeus and Godoy, 2018; Johnson and Bronstein, 2019). Nowadays, two main theories in community ecology are present (Letten, Ke, and Fukami, 2017). The first, contemporary niche theory, is the legacy of Tilman's (1982) resource competition theory. Its origins are established in a mechanistic consumer-resource model (Letten, Ke, and Fukami, 2017). Here, limiting resources are the drivers of coexistence (Chase and Leibold, 2003). The second, modern coexistence theory, follows Chesson (2000) by quantifying the different mechanisms at play in a community of competing species (Ellner et al., 2018). The Lotka-Volterra model is the root of the theory (Letten, Ke, and Fukami, 2017) and coexistence is not driven solely by resource competition, but also by other limiting factors (e.g. environmental conditions) (Chesson, 2000).

Whereas both theories seek to understand how do species coexist, they focus on different aspects. First of all, contemporary niche theory enables the detailed analysis of common models, whereas modern coexistence theory allows a more general application of its principles. Moreover, while contemporary niche theory focuses on the resources responsible for the regulation of coexistence, modern coexistence theory is more interested on the limiting factors influencing the growth rate of a given species. Limiting factors include resources as well as other environmental factor such as spatial space, climate, temperature. Modern coexistence theory offers mathematical frameworks to quantify the phenomenological variables of coexistence in order to answer, "can these species coexist?" (Letten, Ke, and Fukami, 2017). On the other hand, contemporary niche theory has a direct and intuitive ecological meaning, which is missing in the modern coexistence theory (Letten, Ke, and Fukami, 2017; Spaak and Laender, 2018). The focus on resources enables an easier ecological understanding than the evaluation of all limiting factors of

the ecosystem. However, the ecological meaning behind the metrics of modern coexistence theory is an emerging area of research.

1.1 Modern coexistence theory

Modern coexistence theory focused on interaction-based models. Under modern coexistence theory, the interactions within an ecosystem provide insight on why do species coexist (HilleRisLambers et al., 2012). These interactions include the effect of species interactions with other species (interspecific competition) and with themselves (intraspecific competition). Until recently, the interactions considered were limited to the ones within the same guild (i.e between species with overlapping resource requirement), ignoring the interactions mediated through other guilds (e.g. predation, pollination) (Chesson, 2000). The nature of these interactions drives the outcome of competition either toward competitive exclusion or coexistence.

Niche and fitness differences

Competition leads to competitive exclusion when one species drives its opponent to extinction (Hardin, 1960). When the interspecific interaction is stronger than the intraspecific, the growth rate of the weaker population becomes negative as the stronger population approaches equilibrium density (HilleRisLambers et al., 2012; Adler et al., 2018). On the other hand, when interspecific interactions are weaker than intraspecific interactions, both populations limit themselves more than the opponent which leads to coexistence (Sears and Chesson, 2007; HilleRisLambers et al., 2012; Adler et al., 2018). Stronger intra- than interspecific competition translates into a negative frequency-dependence, that is species grow faster when they are rare (i.e. a low abundance), buffering their population against competitive exclusion (Chesson, 2000; HilleRisLambers et al., 2012; Adler et al., 2018). Niche difference quantifies the frequency-dependence of a community (Chesson, 2000; Godoy and Levine, 2014; Spaak and Laender, 2018). In absence of niche difference, fitness difference determines the outcome of competition. Fitness difference is measured the competitive inequalities which promote competitive exclusion (Chesson, 2000; Godoy and Levine, 2014; Spaak and Laender, 2018).

A niche difference smaller than fitness difference leads to competitive exclusion: one species outcompetes another in terms of productivity, reproduction rate, survival rate and other mechanisms, leading to an asymmetric interspecific competition translated by fitness difference (Chesson, 2000). However, niche difference can overcome fitness difference thanks to density-dependent mechanisms which increase intraspecific interactions (Godoy and Levine, 2014; Chu and Adler, 2015). Density-dependent mechanisms include resource partitioning (Tilman, 1982; Chesson, 2000), various spatial and temporal resource requirements (Gause, 1934; Tilman, 1982), density-dependent predation (Chesson, 2000; HilleRisLambers et al., 2012). Niche difference is not an hypervolume, as the ecological niche of a species, but rather a real number. The concept of niche (Grinnell, 1924)) and niche difference as introduced by Chesson, 2000 are only distantly related.

Quantification of niche and fitness differences

Niche and fitness differences are theoretical frameworks that must be translated into empirical tools in order to examine the features relevant to a community's interactions. The first mathematical equation given by Chesson (1990) computed niche difference as the correlation of the resource consumption vectors. Since Chesson (1990), ten additional definitions have been proposed to compute niche and fitness differences. Most definitions have a mathematical framework involving the effect of a population on itself (in monoculture) and on its opponent (see table 2.2). This total of eleven definitions is excessive, especially given that not all ecologists studying coexistence theory are aware of their existence. This large number of different definitions can be explained by the constraints of the population model used and the biological system [2] studied. Model-specific definitions have been proposed for the most used models in theoretical ecology (Chesson, 2000; Chesson and Kuang, 2008; Adler, HilleRisLambers, and Levine, 2007; Godoy, Kraft, and Levine, 2014; Carmel et al., 2017; Bimler et al., 2018). More general definitions have been proposed that can be applied to a wider range of models and experimental settings (Chesson, 2003; Carroll, Cardinale, and Nisbet, 2011; Zhao, Zhang, and Zhang, 2016; Spaak and Laender, 2018). Despite the diverse possibilities to compute $\mathcal{NFD}$[3], all studies available only use one

[2] A biological system represents an assembly of species sharing specific ecological function, e.g. perennial plant, annual plant, phytoplankton, bacteria

[3] $\mathcal{NFD}$ refers to the real number resulting from applying the mathematical definition. Whereas, "niche and fitness differences" refers to the theoretical concepts.

method. This limited application shows the constraints behind having definitions which are system specific.

So far, there is no universally-accepted definition within the scientific community. Hence, $\mathcal{NFD}$ of a community could be measured by different definitions, yielding different qualitative results. For this reason, the ecological meaning and conclusions drawn from $\mathcal{NFD}$ may likely depend on the definitions as well (Spaak and Laender, 2018). At the present time, the link between the practical and theoretical frameworks behind the niche and fitness differences is poorly defined. This confusion may also dissuade the effort of new scientists in the field of coexistence theory. Therefore, even if niche and fitness differences were first conceptualised as the bridge between biodiversity and modern coexistence theory (Carroll, Cardinale, and Nisbet, 2011), now with eleven definitions, they are likely to become the source of divergence.

Ecology behind $\mathcal{NFD}$

Within a biological system, niche and fitness differences give insight into the interactions' characteristics. In theory, they give quantitative results which translate into qualitative interpretations of the interactions in question. However, based on the definition used, the degree of ecological meaning captured differs. The optimum would be to have explicit range indicating the outcome of competition and the interactions at stake. A $\mathcal{ND}$ equal to 0 would translate the absence of frequency-dependence mechanisms (i.e. inter- and intraspecific competitions of each species are respectively equals), whereas a $\mathcal{ND}$ equal to 1 indicates the absence of interspecific competitions. Between 0 and 1, $\mathcal{ND}$ would capture negative frequency-dependence for both species, enabling stable coexistence based on the balance between $\mathcal{ND}$ and $\mathcal{FD}$ (see fig.1.1). When $\mathcal{ND}$ is positive and higher than 1 for at least one species, the species profit from the positive interaction (facilitation), i.e both inter- and intraspecific effects are positive (Adler et al., 2018). On the other hand, a negative $\mathcal{ND}$ would captures a positive frequency-dependence which means that one or both of the species grows faster when already at a high density (see fig.1.1). This prevents the possibility of stable coexistence (Spaak and Laender, 2018; Ke and Letten, 2018).

Concerning $\mathcal{FD}$, it should be specific to the population. The population with the higher $\mathcal{FD}$ would correspond to the inferior competitor. A $\mathcal{FD}$

equal to 0 would translate equal competitive strength for both species (i.e. inter- specific competitions are equals between the species), whereas a $\mathcal{FD}$ equal to 1 means that its invasion growth rate is equal to its monoculture growth rate. If a population has a $\mathcal{FD}$ bigger than 1, it captures its dependence of the other population to survive, such as in a consumers-predators systems. When both $\mathcal{ND}$ and $\mathcal{FD}$ equal 0 (i.e. functionally identical) , the interactions are neutral (Hubbell, 2011). This extreme case of modern coexistence theory encompasses species that have identical $\mathcal{FD}$ and effect on each other (Adler, HilleRisLambers, and Levine, 2007). Under neutrality, the community structure and diversity are based on random walk (e.g. dispersal processes) to extinction (Hubbell, 2011).

Furthermore, the outcome of coexistence should be easily deducible from the value of $\mathcal{NFD}$, when the community includes two populations. Under priority effect, the winner of competition depends upon the starting conditions (Ke and Letten, 2018). Priority effect implies that both populations have a negative $\mathcal{ND}$ and none of the population is strong enough to exclude the other (intermediate $\mathcal{FD}$) (see fig.1.1). Competitive exclusion is observed when both species have a $\mathcal{ND}$ smaller than one (potentially negative) and their $\mathcal{FD}$ is separated by the coexistence threshold. Finally, coexistence requires a $\mathcal{ND}$ bigger than 0 and that both $\mathcal{FD}$ are smaller than $\mathcal{ND}$.

Modern coexistence theory encompasses the diverse interactions found in natural communities. The gradient from neutral to niche-based processes and the $\mathcal{FD}$ scale are inclusive of all type of interactions. Niche and fitness differences should thus offer the features of any interactions driving coexisting communities. Nevertheless, the different definitions imply different frameworks which do not enable the deduction of all interactions or competitive outcomes. For instance, the definition of Carroll, Cardinale, and Nisbet, 2011 does not allow a $\mathcal{ND}$ bigger than 1, it can therefore not analyse communities under complete facilitation (i.e. where the resulting interspecific interaction is positive). Two definitions are also community-specific and not species-specific, which prevents easy identification of the superior competitor or the differentiation between competitive exclusion and priority effect when $\mathcal{ND}$ is negative and $\mathcal{FD}$ is superior to the coexistence threshold (i.e. condition line defined by $\mathcal{FD} = \mathcal{ND}$). On the other hand, some definitions integrate other characteristics such as multispecies interactions (Carroll, Cardinale, and Nisbet, 2011; Saavedra et al., 2017; Spaak and Laender, 2018) or

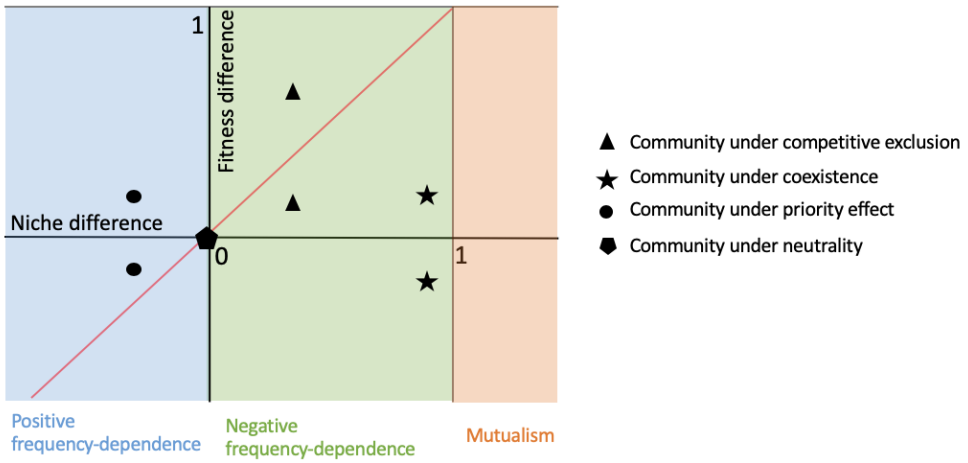

FIGURE 1.1: $\mathcal{FD}$ and $\mathcal{ND}$ of the different ecological interactions' types. Examples of the competitive outcome of four pairwise (i.e. containing 2 populations) communities. Figure inspired from Spaak and Laender (2018).

predator-prey interactions (Carroll, Cardinale, and Nisbet, 2011; Spaak and Laender, 2018).

1.2 Drivers of niche and fitness differences

Niche and fitness differences of a community are driven by the species identities and the surrounding environment. The species identities involve specific functional traits which influence the competitive outcome. The functional traits at stake also depend upon the surrounding environment. Indeed, the ELF interacting with a species are different based on the surrounding environment. Thus, in a given environment, specific functional traits assemble the community interactions. These interactions define $\mathcal{NFD}$ and explain why species coexist (HilleRisLambers et al., 2012).

1.2.1 Species ecology

Recently, a particular focus has been attributed to whether differences or similarities matter the most between two-occurring species. The seeds have been sown by Darwin's naturalisation hypothesis (1859) highlighting the importance of phylogenetic distance between two competing species.

Closely-related species have more functional similarities than distant species (Chesson, 2000; Mayfield and Levine, 2010). That is, small phylogenetic distance between two species is translated by higher functional similarities. Higher similarities between species can reduce both $\mathcal{ND}$ and $\mathcal{FD}$ (Mayfield and Levine, 2010). However, smaller $\mathcal{ND}$ and $\mathcal{FD}$ push the competition outcome in opposite directions: a reduction in niche difference pushes the system toward competitive exclusion whereas a smaller $\mathcal{FD}$ promotes coexistence. Thus, the empirical evidences that phylogenetic distance can predict the outcome of competition is controversial (Mayfield and Levine, 2010; Narwani et al., 2013; Godoy, Kraft, and Levine, 2014; Venail et al., 2014).

On the other hand, the outcome of competition has been linked to functional traits similarity (Narwani et al., 2013; Kraft, Godoy, and Levine, 2015)). Indeed, Conti et al. (2018) proved the correlation of functional similarities and trait hierarchies with respectively niche overlap and differences in competitive strength. Therefore, studying the traits themselves may better identify the mechanisms of coexistence. For example, Gallego, Venail, and Ibelings (2019) showed that $\mathcal{ND}$ and $\mathcal{FD}$ increase with size differences. However, one trait cannot be entirely responsible for the outcome of competition (Kraft, Godoy, and Levine, 2015; Gallego, Venail, and Ibelings, 2019). Competitive outcome involves the combined action of many functional traits (Germain et al., 2018). Kraft, Godoy, and Levine (2015) showed that, contrary to single traits, several functional traits are required to evaluate niche and fitness differences and thus have an estimation of the competitive interactions of the community.

Therefore, the interactions within a community depend upon the specific ecology of its species. Each species has specific functional traits that characterise their interactions with the abiotic and biotic environment (Kraft et al., 2015). Furthermore, the species within a biological system often compete for the same factors. For example, plankton species forming a diverse community compete for a small amount of resource such as light and nutrients. Their remarkable diversity has been described as the result of a wide differentiation along their ability to absorb light, uptake nutrient and avoid grazer pressure (Hutchinson, 1961). In general, competing interactions between species of one biological system may be associated with similar functional traits. Therefore, one biological system should have a specific range of interactions between its species. This range of interactions is captured by specific range

of $\mathcal{NFD}$. To identify the specific functional traits determining this range for one biological system would enhance conservation strategy. For example, to know the functional traits upon which competition relies, could help mitigate exotic invasion. Indeed, knowledge of the functional traits acting on niche and fitness difference between an exotic and native species can enhance the establishment of specific management actions (Godoy and Levine, 2014).

1.2.2 Environmental limiting factors (ELF)

ELF can have both direct and indirect effects on community composition (HilleRisLambers et al., 2012; Cadotte and Tucker, 2017; Wainwright et al., 2018). The direct effect involves the tolerance of species to abiotic conditions, and affects the survival and fecundity of the species. The indirect effect is mediated by species interactions (Wainwright et al., 2016; Matias et al., 2018), and affects the competitive outcomes over environmental gradients. Indeed, environmental gradients creates local patches, between which $\mathcal{ND}$ and $\mathcal{FD}$ change. Hence, an environmental gradient may produce different competitive outcomes in different local patches, impacting the global community composition (Chesson, 2000; Kraft, Godoy, and Levine, 2015; Cadotte and Tucker, 2017; Germain, Mayfield, and Gilbert, 2018; Lanuza, Bartomeus, and Godoy, 2018).

ELF are divided into internal factor and external factors (fig.1.2). External factors influence population functional traits but are independent of the community's density (fig.1.2) (Turchin, 2003; Meszéna et al., 2006). They include factors such as seasonality, temperature, precipitation, pollutant input and water speed. Internal factors of a population are affecting population functional traits and are themselves affected by community's density (fig.1.2) (Meszéna et al., 2006). These factors include for example, moisture, light and soil biota. Every ecosystem includes variables of local, regional and global scales. For each population of an ecosystem, the variables can be categorised based on their interactions with the population dynamics (Chesson, 1994; Meszéna et al., 2006). Internal and external factors represent an exclusive description of the environmental parameters influencing community interactions (Meszéna et al., 2006). Their influence on the community is reflected in the $\mathcal{NFD}$ of the community.

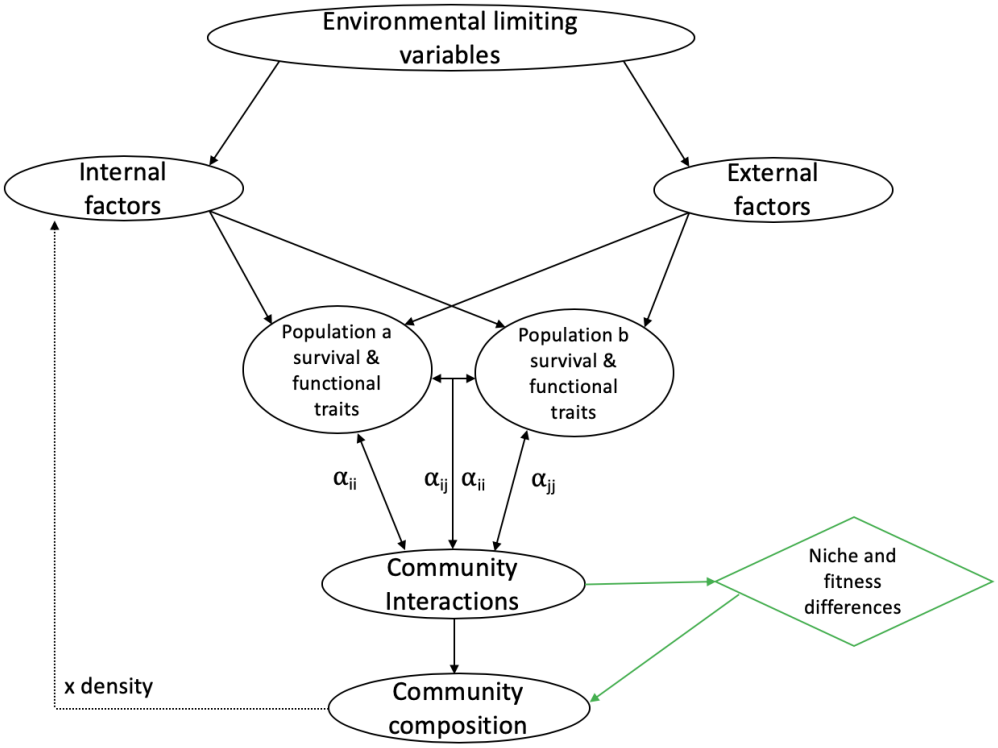

FIGURE 1.2: Community composition is determined by both direct and indirect effects of ELF and species identity. The species identity defines how a environmental factor affects its survival (direct effect) and its functional traits (indirect effect). Species identity also influences its intraspecific ($_{ii}$ and $_{jj}$) and interspecific ($_{ij}$ and $_{ji}$) interactions. These interactions drive the $\mathcal{NFD}$ of the community. Hence, $\mathcal{NFD}$ captures the interactions responsible for community composition, which then affects the internal factors. The effect of the internal factors is influenced by the population density of the species within the community.

Gradient of ELF

Nowadays, climate change and anthropogenic activities (nutrient pollution, landscape use, climate change, etc) perturb ELF (Cardinale et al., 2012; Valladares et al., 2015; Cardinaux, Hart, and Alexander, 2018). Perturbations act either negatively or positively on the population's inter- or/and intraspecific interactions. Perturbations, therefore, have a cascade effect on community composition. The direction and path of the reaction depend upon the identity of the perturbations and of the community concerned.

The perturbation acts on niche and fitness differences of the community. For example, in an alpine environment, an increase in temperature (an external factor) can increase the fitness of subalpine species to the detriment of alpine species' fitness (Parolo and Rossi, 2008). Moreover, a location encountering a homogenisation by the deposition of nitrogen (internal factor), favouring a few nitrogenous species at the cost of many species adapted to infertile condition (Stevens, 2004; Southon et al., 2013). Environmental homogenisation by anthropogenic activities is one of the main causes of biodiversity loss (Götzenberger et al., 2012; Valladares et al., 2015). In general, a change in the environmental heterogeneity can alter local competitive outcomes by promoting species that have greater competitive ability due to a phenotype that is better adapted to the perturbed environment (Zavaleta et al., 2003; Parolo and Rossi, 2008; Valladares et al., 2015). Thus, changes in ELF influence community asynchronously based on the functional traits at stake (Zavaleta et al., 2003). Thus it is essential to assess the relevant functional traits of a biological system across different environments. This assessment will enable an accurate forecast of how anthropogenic activities and climate change influence community interactions within this biological system.

1.2.3 Interactions of ELF changes and species ecology

Niche and fitness differences are influenced by several factors, including species identity and internal/external factors, which affect the direction and strength of the interactions in the community. It is important to consider these factors individually as well as in combination. Evaluating the scale and strength of one factor is essential to identify its specific effect on community assembly in a given environment (Napier, Mordecai, and Heckman, 2016; Cardinaux, Hart, and Alexander, 2018; Matias et al., 2018; Petry et al., 2018). However, research which conjugates factors gives critical insight on

how they interact to influence community assembly (Silvertown, 2004; Bimler et al., 2018; Lanuza, Bartomeus, and Godoy, 2018). Until now, research has mainly focused on the individual effects of internal or external factors on different species of the same biological system. Gradients of internal factors, considering both abiotic and biotic variables, are more often studied, thanks to their ease of experimental implementation. Within the annual and perennial plant systems, the abiotic factors considered until now include the effect of soil biota (Cardinaux, Hart, and Alexander, 2018), nutrient availability (Wedin and Tilman, 1993; Hautier, Niklaus, and Hector, 2009) and water availability (Wainwright et al., 2019). The effect of internal abiotic factors on niche and fitness differences depends upon the ecology of the species concerned. For instance, eutrophication affects $\mathcal{ND}$ and $\mathcal{FD}$ of grasslands not by the intermediary of soil resource competition, but rather by increased competition for light (Hautier, Niklaus, and Hector, 2009). The species identity is thus important to understand the effect of an internal abiotic factor on $\mathcal{ND}$ and $\mathcal{FD}$. On the other hand, studies of the effect of biotic factors on $\mathcal{ND}$ and $\mathcal{FD}$ are comparatively uncommon. Examples exist mostly within the annual plant system, such as the role of ants on seed loss Petry et al., 2018 or floral visitors on reproductive success Lanuza, Bartomeus, and Godoy, 2018. The scarcity of research on internal biotic factors may be overcome by the recent combination of network theory and niche theory (Godoy et al., 2018). This combination will enable the translation of, for example, ants and floral visitors, from biotic factors towards constituents of the community.

Gradients of external factors also depend on species ecology. However, research concerned with this is scattered due to the complex experimental methodology required (Bimler et al., 2018; Matias et al., 2018). Nevertheless, the studies that create an external environment gradient demonstrate a correlation between species ecology and the effect of the environmental gradient (Bimler et al., 2018; Matias et al., 2018).

To date, research has solely focused on the interaction between species identity and the effect of a single environmental factor, rather than multiple factors. However, in nature, they interact to shape ecosystems. In some cases, this interaction can be complementary: Southon et al. (2013) showed that the effect of nitrogen-deposition on plant species richness is greater when coupled with higher temperature. In others, it can be opposing: Napier, Mordecai, and Heckman, 2016 found that the effect of drought on the competitive

abilities of two grass species was mitigated by herbivory. The change in $\mathcal{NFD}$ cause by the effect of the external factor is mitigated by the simultaneous change of $\mathcal{NFD}$ provoked by the effect of the internal factor. Hence, multiple environmental factors can have complementary or opposing effects on $\mathcal{ND}$ and $\mathcal{FD}$ (Lanuza, Bartomeus, and Godoy, 2018). In general, the individuals effect of these factors is dependant on the species identities within the community. Even if we can forecast the direction and strength of their individual effect on $\mathcal{NFD}$, we cannot predict their combined effect, as it depends on the nature of their interactions and the species identities. Further research, involving specific combinations of environmental factors, needs to focus on how combined multiple environmental factors act on niche and fitness differences of a specific community.

1.3 Objectives and hypothesis

The objective of this work is to identify the influences of environmental gradients (1.3.1) and species identities (1.3.2) on niche and fitness differences. To achieve this, we have taken two approaches: an experiment and a meta-analysis of the present literature.

1.3.1 Niche and fitness differences across environmental gradients

Our first objective (obj.1) is to identify how a combination of gradients of internal and external factors affect community composition, in comparison to their individual effects. We hypothesise (hyp.1.1) that an internal factor can mitigate the negative effect of an external factor. We expect that the combined effect of internal and external factors will have a monotone or linear response on $\mathcal{ND}$ and $\mathcal{FD}$ (fig.1.3).

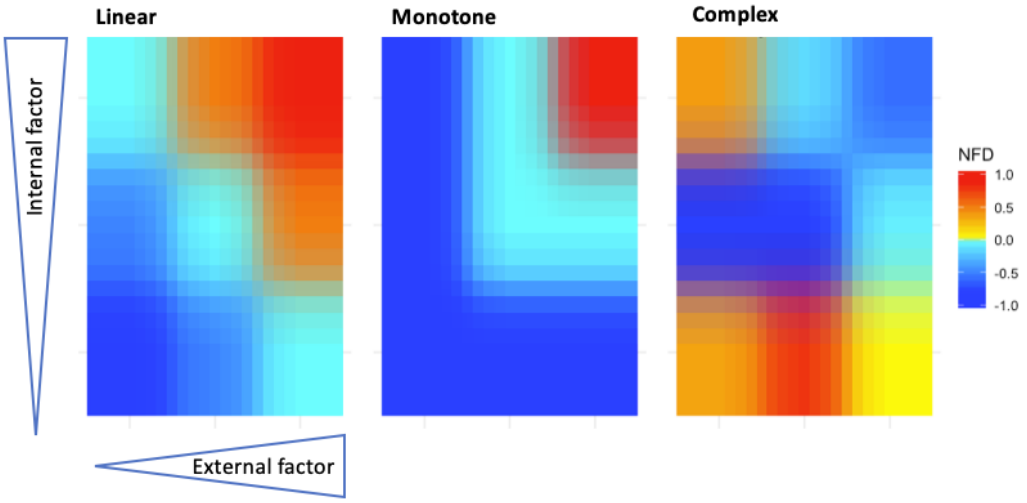

FIGURE 1.3: Possible interactions between gradients of internal and external factors on $\mathcal{ND}$ and $\mathcal{FD}$. The effect of their interaction can be: **linear**: the effect of the external and internal factors are summed, each community is affected identically by the gradient of the external factor, regardless of the gradient of the internal factor; **monotone**: the external and internal factors interact positively, each community is affected differently by the gradient of the external factor, based on the gradient of the internal factor; **complex**: the interaction between the internal and external factors do not follow a regular pattern.

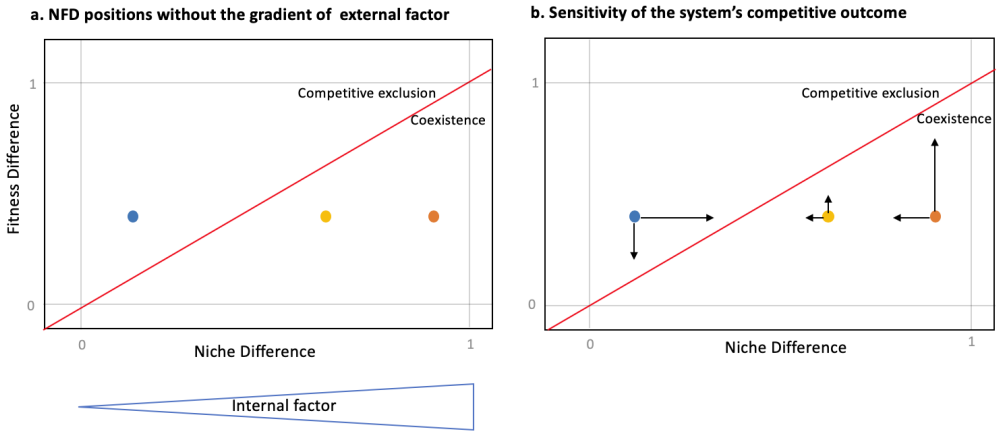

FIGURE 1.4: A gradient of the internal factor (with three levels) applied to otherwise identical communities causes them to have different $\mathcal{ND}$ (panel **a**). The sensitivity of the community's competitive outcome varies with the intensity of the internal factor, changes that the external factor increase could induced. The intensity and direction of the external factor required to change the community composition varies with the intensity of the internal factor. The arrows illustrate the sensitivity of the community's competitive outcome. The smaller the arrow, the higher the sensitivity of the community in that direction (panel **b**).

The external factor has a negative impact on survival and, therefore, $\mathcal{FD}$ should decrease with increasing intensity of this external factor. It is assumed that the gradient of the internal factor will create heterogeneity in the environment which should mainly impact $\mathcal{ND}$. The gradient of the internal factor should give different values of $\mathcal{ND}$ ranging between 0 and 1 (fig.2.2.a). The value of $\mathcal{ND}$ given by the internal factor may influence the effect of the external factor on the community's competitive outcome. A high value of $\mathcal{ND}$, given by the high heterogeneity, should decrease the sensitivity of the community's competitive outcome to a change of $\mathcal{FD}$ (fig.2.2.b). That is, as the gradient of the external factor impacts $\mathcal{FD}$, the community with the highest niche difference should be more resistant against its effect. On the other hand, a community with small niche differences is more susceptible to changes in competitive outcomes via changes in $\mathcal{FD}$. However, if the increase of the external factor also affects $\mathcal{ND}$, the sensitivity of the community's competitive outcome is reversed. In any case, the most sensitive community is the one nearest the coexistence threshold. Overall, if the internal and external factors interact in a monotone or linear fashion, the internal factor may mitigate the effect of the external factor.

1.3.2 Niche and fitness differences across biological systems

Our second objective (obj.2) is to compare the type of ecological interactions (e.g. mutualism or negative/positive frequency-dependence) of four biological systems and their respective determinant of coexistence (niche difference and/or fitness difference). We performed a meta-analysis of the current literature to gather a list of empirical papers computing $\mathcal{NFD}$ with one of the eleven definitions. Among these papers, four biological systems are present: perennial plant, annual plant, bacteria and plankton. In order to compare their $\mathcal{NFD}$ distribution, we computed three definitions, allowing inter-system comparisons, as they can be applied to any community model and even empirical data.

Our first hypothesis (hyp.2.1) is that the interaction type will be different based on the biological system studied, but not based on the definition used. Indeed, the three definitions will naturally lead to different quantitative values of $\mathcal{NFD}$, as they have different mathematical definitions. Nevertheless, we expect to see the same qualitative results, as they all quantify the same concept ($\mathcal{NFD}$). Moreover, the four biological systems involve different environments (terrestrial and aquatic) which imply different ecology (life span, resource uptake strategy, trait plasticity, etc.). We expect that their different specific ecology will have different $\mathcal{NFD}$ distributions, which capture different interactions. Their specific ecology defines the trait diversity of the biological system. Some biological systems, with greater trait diversity, are therefore capable of having greater diversity of interaction types. Thus, the specific ecology of a biological system emphasises different intra- and interspecific interactions, which determine its niche and fitness distribution.

Our second hypothesis (hyp.2.2) is that, within one biological system, the difference of the distributions of $\mathcal{ND}$ and $\mathcal{FD}$ between its coexisting and non-coexisting communities reflect the system's ecology. For instance, all species within a biological system may have different resource uptake strategies but similar reproductive strategies, conferring potential for high $\mathcal{ND}$ but small $\mathcal{FD}$ between all species. Communities like this, will thus have similar distribution of $\mathcal{FD}$, whether they are coexisting or not, but higher $\mathcal{ND}$'s distribution for coexisting communities. In this case, coexistence would only be dependant on $\mathcal{ND}$.

Furthermore, we considered all species of one biological system, regardless of their respective environment. In other words, we don't focus on the influence of the different internal and external factors on $\mathcal{NFD}$, but rather on the general ecology of these biological systems. We did not attribute the interaction types of one biological system to specific functional traits. However, our inter-system comparison opens the road toward future trait-based comparisons.

Chapter 2

Methods

2.1 Niche and fitness differences across environmental gradients

2.1.1 Environmental gradients

We assess the combined effect of gradients in an external and internal factor for a community including two sub-species of cyanobacteria (*Synechococcus sp.*): BS4 and BS5 (biological system is phytoplankton). Different concentrations of a pollutant (atrazine) create a gradient of an external factor. A treatment at a specific level of the gradient, the atrazine concentration was kept relatively constant. That is, it is not affected by the density of phytoplankton as we renewed the medium regularly. Thus we can consider it an external factor. Along an increasing concentration of the pollutant, we expect $\mathcal{NFD}$ to decrease. $\mathcal{FD}$ should decrease due to the effect of atrazine on phytoplankton photosynthetic efficiency (fig.2.1). Even if atrazine does not affect phytoplankton absorption spectrum (fig.2.1), it could potentially affect $\mathcal{ND}$ by the inhibition of the second photosystem, which would affect their resource uptake efficiency (i.e. number of photon converted into biomass).

The gradient of the internal factor is created by different light regimes. Phytoplankton contains specific photosynthetic pigments, conferring them a specific light absorption spectrum (Stomp et al., 2004). Under white light, this photosynthetic characteristic establishes a niche difference between populations with different pigments. Populations differentiate themselves also by their specific photosynthetic efficiency, which is their ability to translate one photon's energy into the population growth rate (Stomp et al., 2004). The spectrum of the incident light therefore influences the growth rate of a species based on its own specific absorption spectrum and photosynthetic efficiency. Incident light covering a larger spectrum corresponds to more

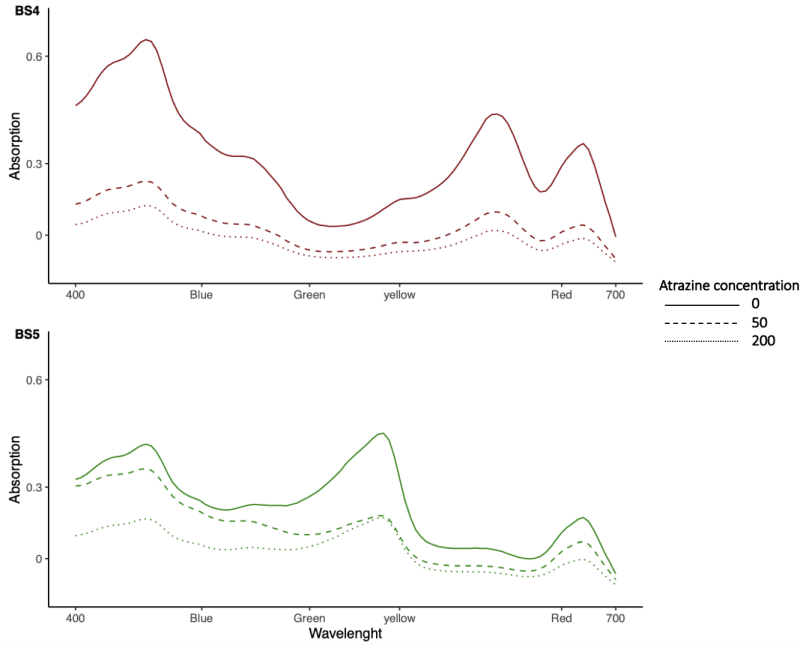

FIGURE 2.1: The atrazine affects their total absorption, but not their relative absorption. Light absorption ($e-05.mul/cells.cm^{-1}$) spectrum of both strains (BS4 and BS5) under $0\mu g/L$ atrazine (full line), $50\mu g/L$ atrazine (dashed line) and $200\mu g/L$ atrazine (dotted line). The absorption spectra were measured using a spectrometer.

heterogeneous environment, which is captured by larger niche opportunities. Thus, the communities should have different $\mathcal{ND}$ based on the incident light characteristics (fig.2.2.a). The two strains of phytoplankton respectively favour light absorption in the red (BS4) and green (BS5) spectrum (see fig2.1). An environment composed of only red and green light should lead to a high $\mathcal{ND}$, as the populations have different pigments, allowing them to avoid competition for light. Conversely, the more we increase blue light, the lower $\mathcal{ND}$ should be, as both species only used chlorophyll-a to absorb blue light (Stomp et al., 2004). The internal factor limits their respective growth, decreasing their $\mathcal{ND}$, as they are in more direct competition for the resource. Thus, the increase of blue light and decrease of red and green light create the gradient of the internal factor. Moreover, we assume that the two strains compete only for light (i.e. photons). Then, for an identical total light intensity, which gives them the same relative amount of photons, the $\mathcal{FD}$ of the superior competitor (fig.2.2.a) should be equal across environments. However, if the light intensity is lower (fewer photons), competition for light is stronger, which may impact the $\mathcal{FD}$ of the community.

We kept constant the other environmental limiting factors (e.g. nutrients and temperature), in order to only observe the combined effect of changes in the light regime and atrazine exposure on $\mathcal{NFD}$.

2.1.2 Computation of niche and fitness differences

Two different general definitions of niche and fitness were computed: Spaak and Laender, 2018 and Carroll, Cardinale, and Nisbet, 2011 (See section 2.2.4 for the mathematical descriptions). Both exclude the use of a pre-defined population model. The required parameters are the monoculture growth rates and the invasive growth rates. The computation of more than one definition maximises the confidence of the results. The detailed script can be found in annex.

2.1.3 Experimental design

We performed a controlled microcosm experiment with two *Synechococcus* (cyanobacteria) strains (BS4 and BS5) to compute $\mathcal{NFD}$. We cultured two cyanobacteria strains in 6-well plates containing 5 ml of sterile brackish medium, with different concentrations of atrazine ($0\mu g/L$, $50\mu g/L$, $200\mu g/L$) under four light settings (blue; red-green; white high; white low (see Fig.2.1)).

The well plates were respectively inoculated with one of the two cyanobacteria strains at two starting concentrations, one low and one high (see Appendix B for the respective growth rate of the cultures over time). Measurements were taken twice a week (approximately every 84 hours) together with medium renewal (10% renewed each time) for 6 weeks. Sampling of community densities were performed using a flow cytometer and analysed using EM clustering with Gaussian multivariate distributions on R (version 3.6.0). The experiment was conducted at 20°C. When the cultures had reached equilibrium (i.e. the initially low-concentration population is of equal density to the initially high-concentration population), we proceeded with the invasion of a host population with the other strain.

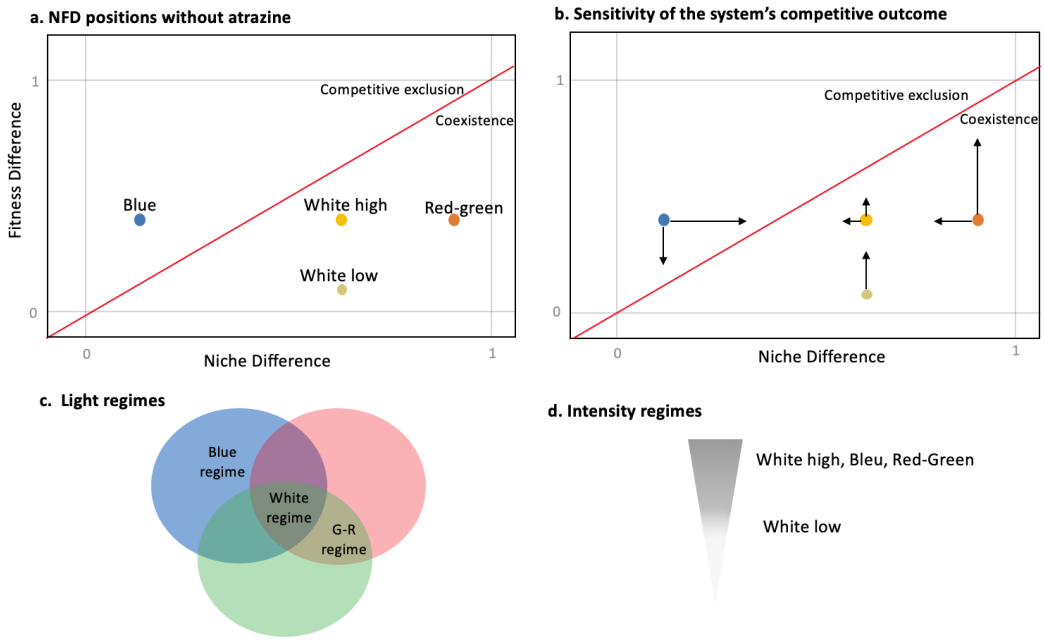

FIGURE 2.2: A gradient of the internal factor (with three levels) applied to otherwise identical communities causes them to have different $\mathcal{ND}$. The sensitivity of the community's competitive outcome varies with the intensity of the internal factor, changes that the external factor increase could induced. The intensity and direction of the external factor required to change the community composition varies with the intensity of the internal factor. The arrows illustrate the sensitivity of the community's competitive outcome. The smaller the arrow, the higher the sensitivity of the community in that direction (panel **b**). In order to create different initial $\mathcal{NFD}$, we considered four different light settings following a gradient from blue to red and green (panel **c**). The blue regime corresponds to a more homogeneous environment than the red-green regime. The treatments always give the same amount of light resource for both species. The fourth (White - low) has a lower amount of light intensity changing the total amount of light resource (panel **d**). The white regime is a mix between blue, red and green light, hence, it does not correspond to white light *per se*.

TABLE 2.1: Experimental settings of each light regime and the heterogeneity it creates.

Regime	Approximation of heterogeneity degree	Settings (in μmol.photon/m^2/s)
Green - Red	Maximal	5 of red light and 15.3 of green light
White - high	Intermediary	2.5 of red light, 7.65 of green light and 12.32 of blue light
White - low	Intermediary	1.25 of red light, 3.8 of green light and 6.15 of blue light
Blue	Minimal	23 of blue light

2.2 Niche and fitness differences across systems

2.2.1 Data acquisition from literature

We performed a literature search for the eleven initial papers introducing a definition of niche and fitness differences. When the number of citations were above 80 (Chesson, 2000; Adler, HilleRisLambers, and Levine, 2007; Chesson and Kuang, 2008), the results of the search were reduced using the following key words: ("niche differences" OR "niche overlap" OR "stabilizing mechanisms") AND ("fitness differences" OR "fitness " OR "equalizing mechanism") AND ("Experiment" OR "Data" OR "Field") AND ("Competition" OR "Coexistence"). Only research-type articles which measured $\mathcal{ND}$ or $\mathcal{FD}$ experimentally using one of the eleven definitions were considered. Out of the eleven definitions, only 7 were computed based on experimental data. Indeed Chesson, 2003, Chesson and Kuang, 2008, Adler, HilleRisLambers, and Levine, 2007 and Carmel et al., 2017 introduced definitions that are primarily theoretical and impractical to use within an empirical study. For each article, we extracted any species-specific growth parameters available (competition coefficient, sensitivity, mono-culture growth rate, invasion growth rate, etc.) as well as the taxonomy. See appendix A to see further details about the data set gathered.

2.2.2 Conversion of data

Based on the estimated parameters of each paper, we computed three general $\mathcal{NFD}$ definitions detailed below (see section 2.2.4). The three definitions were chosen out of the eleven as they associated minimal mathematical and biological restrictions. Indeed, none of them require the use of a specific population model as they were not created to satisfy a specific system. However, mathematical restrictions are still present which prevent us having the same number of communities for each definition.

Furthermore, not all papers had the required estimated parameters. For example, papers that use the definition of Carroll, Cardinale, and Nisbet (2011) did not provide the required measurements to compute the definition of Zhao, Zhang, and Zhang (2016). Hence, we do not have any values for the phytoplankton system according to Zhao, Zhang, and Zhang (2016), as all initial papers used the definition of Carroll, Cardinale, and Nisbet (2011). We had to only consider the $\mathcal{FD}$ of the inferior competitor for all definitions.

Both Zhao, Zhang, and Zhang (2016) and Spaak and Laender (2018) enabled the computation of a population-specific $\mathcal{FD}$, however, Carroll, Cardinale, and Nisbet (2011) does not. To prevent the distributions of Zhao, Zhang, and Zhang (2016) and Spaak and Laender (2018) to have twice the number of communities present in the distribution of Carroll, Cardinale, and Nisbet (2011), we only kept the FD_z (i.e. $\mathcal{FD}$ according to Zhao's definition) and FD_s (i.e. $\mathcal{FD}$ according to Spaak's definition)of the inferior competitor.

Finally, the computation of Spaak's definition using papers that used the definition of Carroll required an approximation. First, we concentrated the search into a rectangle defined as $1 - S_i < ND_s < 1 - S_j$ and $0 < FD_s < 1 - \frac{S_i}{S_j}$ (i.e. S_i are the sensitivities computed in the scope of Carroll's definition, see below). Then, within this range, we can determine the possible values of FD_s using the following equation:

$$FD_{s,i} = \frac{(1 - S_i) - ND_s}{ND_s} \tag{2.1}$$

The equation 2.1 referred to a curve delimited by the range of the rectangle. On this line we randomly chose 10 points to represent NFD_s (i.e. $\mathcal{NFD}$ according to Spaak's definition) of the community.

2.2.3 Full factorial analysis of the data

We split the computed $\mathcal{NFD}$ into different subsets with the following three factors: biological system (phytoplankton, bacteria, annual plant, perennial plant), definition applied (Spaak, Carroll, Zhao) and outcome of competition (coexistence, priority effects, competitive exclusion). The respective coexistence conditions of each definition are indicated in their descriptions. As the definitions differ mathematically, we focused on qualitative differences between the subsets, not on numerical differences.

2.2.4 Definitions' frameworks

We chose the three most general definitions of the eleven available, which enabled comparison between their results. These three definitions include the minimum restrictions in terms of model requirement, and estimated parameters needed (see tab 2.2 to see all definitions and their respective restrictions). The entire analysis and computation were done with R (version 3.6.0). The detailed script can be found in annex.

Spaak and Laender, 2018

This definition does not require the use of any population model. The growth rates were obtained by the fit of a univariate spline through the data with the code available at Spaak and Laender, 2018.

We can define the community model as a function of the densities of respectively species i and species j.

$$\frac{1}{N}\frac{dN}{dt} = f_i(N_i, N_j) \tag{2.2}$$

The ND_s of a population accounts for the effect of both its own population and the population of its competitor on its growth rate. From the respective effects, we remove the effect of species i on itself when there is no frequency-dependence.

$$ND_s = \frac{f_i(0, N_j^*) - f_i(c_j N_j^*, 0)}{f_i(0,0) - f_i(c_j N_j^*, 0)} \tag{2.3}$$

$$FD_s = \frac{-f_i(c_j N_j^*, 0)}{f_i(c_j N_j^*, 0) - f_j(N_j^*, 0)} \tag{2.4}$$

$f_i(0, N_j^*)$ is the invasion growth rate, $f_i(0,0)$ is the monoculture growth rate and $f_i(c_j N_j^*$,0) is the no-niche growth rate. The no-niche growth rate removes the strength of frequency-dependence for a focal species i. The factor c_j quantifies the difference in total dependence on all limiting factors, which is needed to convert the density of j to the density of i (Spaak and Laender, 2018). We rearranged the equation FD_s to simplify the comparison. From the original definition we apply $1 - 1/FD_s$ and considered that the second term of the original definition was equal to zero (see tab.2.2 for the original definition).

The niche and fitness differences are specific for each species of the community. The species with the highest FD is the inferior competitor. Persistence of both species implies $FD_s \leq ND_s$ and a positive ND_s. Priority effect arises if both species have $FD_s < ND_s$ and a negative ND_s. All other possibilities correspond to competitive exclusion of the inferior competitor by the superior competitor.

Carroll, Cardinale, and Nisbet, 2011

The definition of Carroll, Cardinale, and Nisbet (2011) does not require the use of any population model. The experiment should provide the necessary growth rate parameters to compute the sensitivities.

$$S_i = \frac{f_i(0,0) - f_i(0,N_j^*)}{f_i(0,0)} \tag{2.5}$$

As before, $f_i(0,0)$ is the invader's growth rate without a competitor and $f_i(0,N_j^*)$ is the invader's growth rate in the presence of species j at its monoculture equilibrium. S_i is limited to 0, as Carroll's definition is only usable when true competition occurs (i.e. the invading species always has a negative effect on its opponent). Interspecific facilitation (i.e positive interactions between competing species) is encountered only when the negative intraspecific interaction is stronger. Niche difference is the geometric mean of the set of sensitivities. Its range is $[-\infty, 1]$.

$$ND_c = 1 - (S_i^{1/n} + S_j^{1/n}) \tag{2.6}$$

n is the total number of species is the communities, here 2. with $S_i \leq S_j$. FD_c is the geometric standard deviation of the set of sensitivities. Its range is $[1, \infty]$. In order to simplify the comparison, we reorganised the original FD_c (see tab.2.2) as 1-1/FD_c. This way, ND_c and FD_c have the same scale and a linear relationship.

$$FD_c = 1 - \frac{S_j}{S_i} \tag{2.7}$$

When transformed, Spaak and Carroll's definitions establish similar ecological thresholds for coexistence. First, they have the same stable coexistence condition $FD_c \leq ND_c$ (additionally, both sensitivities are smaller than 1 for Carroll). Second, the niche and fitness-axis implies the same interaction types: positive ND indicates negative frequency-dependence, negative ND indicates positive frequency-dependence, a zero ND means that the competitor have inter-specific competitions equal to 0 , a zero FD means that the competitors have the same competing strength. However, as the ND_c and FD_c are common for the species of the community, FD_c is always positive and corresponds to the inferior competitor. When ND_c is negative, it is impossible to distinguish competitive exclusion from priority effects by examining the FD_c, as it is only computed for the inferior competitor. To determine

the outcome of competition, we need to look at the respective sensitivities of the species : $S_i > 1$ and $S_j > 1$ equals priority effect, $S_i < 1$ and $S_j < 1$ equals coexistence, and the other alternatives correspond to competitive exclusion. NFD_c can theoretically be computed for multi-species communities, but there is no coexistence condition.

Zhao, Zhang, and Zhang, 2016

Originally, Zhao's definition was intended to be used as link between empirical work and coexistence theory, not as a new definition of $\mathcal{NFD}$, which would enable the identification of the community's interactions. In fact, the definition is less practical because only a few values of NFD_z capture an ecological meaning. For example, Spaak's NFD_s is 0 if and only if we have neutrality, however, in Zhao, neutrality implies NFD_z equals to 0 (one with the original definition), but ND_z equals to 0 does not imply neutrality. Thus, their definitions don't encompass important ecological interactions. Nevertheless, as they defined the same ecological concept that are niche and fitness difference, we should still find the same relation between the biological system.

ND_z is originally defined as the ratio of relative growth rates when considering respectively the interspecific and the intraspecific competition.

$$ND_z = \frac{f_i(0, N_j^*) + f_j(0, N_i^*)}{2} \tag{2.8}$$

Once again, we rearranged the definition (subtracted 1 and divided by 2) in order to define 0 as the no-niche differentiation value for all three definitions. FD_z is defined as the ratio between the species' respective environmental carrying capacities, which are similar to the ratio of their respective equilibrium densities.

$$FD_z = \log_{10}\left(\frac{N_i^*}{N_j^*}\right) \tag{2.9}$$

ND_z and FD_z have the same range: $[-\infty, \infty]$.

ND_z is common for the two competing species, but not FD_z. Zhao's definition does not allow the determination of the outcome of competition given ND_z and FD_z . However, we can distinguish coexisting communities from non-coexisting communities when both competitors have a positive invasive growth rate (Zhao, Zhang, and Zhang, 2016). On the contrary, when both have a negative invasion growth rate, this indicates priority effects.

TABLE 2.2: The 11 definitions, their frameworks, their restrictions and the number of experimental papers associated. The symbols correspond to: α_{ij} interaction coefficients, according to the Lotka-Volterra model; a_{ij} interaction coefficients, according to the Annual plant model; λ_i per-germinant fecundity in the absence of competition according to the Annual plant model ; K_i environmental carrying capacity of species i; k_{A1} is the per capita rate at which species A consumes resource 1

paper	Assumption	mathematical definition	Experiment and requirements	Number of papers applying this definition
Chesson and Kuang, 2008	Mac-Arthur model with predator extension	$ND = 1 - \frac{\sqrt{\alpha_{ij}^R \alpha_{ji}^R} + \sqrt{\alpha_{ij}^R \alpha_{ji}^R}}{s_i s_j}$ $FD_i = \frac{s_j}{s_i} \frac{\mu_i^R - \mu_i^P - m_i}{\mu_j^R - \mu_j^P - m_j}$	Model fitting	
Chesson, 1990	LV-model	$ND = 1 - \sqrt{\frac{a_{ij} a_{ji}}{a_{ii} a_{jj}}}$ $FD_i = \sqrt{\frac{a_{ji} a_{jj}}{a_{ij} a_{ii}}}$	Model fitting	2
Adler, HilleRisLambers, and Levine, 2007	Annual plant model	$ND_i = \log\left(\frac{\lambda_j}{1 + \frac{a_{ij}}{a_{jj}}(\lambda_j - 1)}\right)$ $FD_i = \log(\frac{\lambda_i}{\lambda_j})$	Model fitting	1
Godoy, Kraft, and Levine, 2014	Annual plant model	$ND = 1 - \sqrt{\frac{a_{ij} a_{ji}}{a_{ii} a_{jj}}}$ $FD_i = \frac{\eta_j - 1}{\eta_i - 1} \sqrt{\frac{a_{ji} a_{jj}}{a_{ij} a_{ii}}}$	Model fitting	10
Bimler et al., 2018	Exponential Annual plant model	$ND = 1 - \sqrt{\frac{\exp a_{ij} + a_{ji}}{\exp a_{ii} + a_{jj}}}$ $FD_i = \sqrt{\frac{\exp a_{ji} + a_{jj}}{\exp a_{ij} + a_{ii}}}$	Model fitting	1
Saavedra et al., 2017	Linear species interactions	$ND = \frac{2}{\pi}\left(\arcsin \frac{\alpha_{ii}\alpha_{jj} - \alpha_{ij}\alpha_{ji}}{\sqrt{\alpha_{ii}2 + \alpha_{ji}2}\sqrt{\alpha_{jj}2 + \alpha_{ij}2}}\right)$ $FD = \frac{180}{\pi}\left(\arccos \frac{r.r_c}{\lVert r \rVert . \lVert r_c \rVert}\right)$	Model fitting	1

Chesson, 2003	Invasion analysis possible, Community model available	$ND = \overline{\frac{\Delta I - N}{d}}$ $FD_i = \frac{r_i}{d_i} - ND$	Model fitting	
Carmel et al., 2017	Invasion analysis possible, Minimal growth rate is equal to mortality	$ND = 1 - min(\frac{k_{A1}/k_{A2}}{k_{B1}/k_{B2}}, \frac{k_{B1}/k_{B2}}{k_{A1}/k_{A2}})$ $FD_i = min(\frac{k_{A1}k_{A2}}{k_{B1}k_{B2}}, \frac{k_{B1}k_{B2}}{k_{A1}k_{A2}})$	Invasion growth rate, Mortality rate	
Zhao, Zhang, and Zhang, 2016	Invasion analysis possible	$ND = 1 + r_i + r_j$ $FD_i = \log_{10}\left(\frac{K_i}{K_j}\right)$	Invasion growth rate, Equilibrium abundancy	1
Carroll, Cardinale, and Nisbet, 2011	Invasion analysis possible	$ND = \frac{f_i(0,N_j^*) - f_i(c_j N_j^*,0)}{f_i(0,0) - f_i(c_j N_j^*,0)}$ $FD = \frac{-f_i(c_j N_j^*,0)}{f_i(c_j N_j^*,0) - f_i(N_j^*,0)}$	Invasion growth rate, Monoculture growth rate	6
Spaak and Laender, 2018	Invasion analysis possible	$ND_i = \frac{f_i(0,N_j^*) - f_i(c_j N_j^*,0)}{f_i(0,0) - f_i(c_j N_j^*,0)}$ $FD_i = \frac{f_i(c_j N_j^*,0)}{f_i(0,0)} - \frac{f_i(N_j^*,0)}{f_j(0,0)}$	Density over time in monoculture, Invasion growth rate	

Chapter 3

Results

3.1 Niche and fitness differences across environmental gradients

The effect of the internal and external factors changed the outcome of competition by increasing FD_s equivalence (i.e. the difference between the FD of both competitor is reduced) and increasing $ND_{s,c}$.

The FD of both competitors became more equivalent and the identity of the superior competitor changed. In the absence of atrazine, BS5 was the superior competitor, regardless of the light regime (see fig3.1 Spaak,BS5-BS4; Carroll only shows the inferior competitor). However, its competitive strength was influenced by the light regime. The blue and white-low regimes created communities where the FD of BS5 is less important than in the red-green and white-high regimes. Its competitive strength decreased when the competition for resource (blue light and light intensity) rose. BS5 is hence more sensitive to the light homogenisation. BS5 also showed an increase of its FD_s along the increasing gradient of atrazine exposure. Actually, under 200 $\mu g/L$ atrazine, the blue regime showed the most variation, which indicates high sensitivity of BS5 for both atrazine exposure and homogenisation of the environment. At 200 $\mu g/L$ atrazine, BS4 was the superior competitor in all communities. This increase of FD equivalence was accompanied by an increase of $\mathcal{ND}$. Both $ND_{c,s}$ increase thanks to a change of frequency-dependence mechanisms (fig3.1). At 0 $\mu g/L$ atrazine, all communities have a negative $ND_{c,s}$ (i.e. the interspecific competition is stronger than intraspecific competition) which implies a positive frequency-dependence (i.e. species grows faster when abundant) (Spaak and Laender, 2018). The communities at the intermediary state of atrazine concentration had a higher, although still negative, $ND_{c,s}$. However, they contained high amounts of variation due to

experimental noise. At 200 $\mu g/L$ atrazine, communities had a mainly positive $ND_{c,s}$ (i.e the intraspecific competition was stronger than interspecific competition) which implies a negative frequency-dependence. The only exception is the red-green regime, which, according to Spaak's definition, is negative but close to zero (fig.3.2, A.1). In most communities, the environmental gradients changed the sign of the frequency-dependence. Therefore, the interaction of the internal and external factors reduced interspecific competition, but increased intraspecific competition, enabling different competitive outcomes. Indeed, under high concentrations of atrazine, the competitive outcomes included coexisting communities for both definitions (fig3.3). The interaction of the internal and external factors thus increased the diversity.

The effects of external and internal factor interact in a complex way. Both niche and fitness differences are not influenced linearly or with a monotone trend by the factors' interaction (fig.3.2). According to Spaak's definition, at 50 $\mu g/L$ atrazine, they are no signs of a ND_s increases, rather a quarter of the communities' ND_s actually decreases (fig.3.2 A.1). ND_s only increases at 200 $\mu g/L$ atrazine and for three quarters of the communities. Hence, ND_s do not increase regularly with the increase gradient of atrazine. ND_c also shows unpredictable trends according to Carroll's definition (fig.3.2 A.2). Concerning the FD_s, the light regimes do not apply a systematic change with the increase gradient of atrazine (fig.3.2 B.1 C.1). Actually, the FD_s of the blue and white-low regime do not change at all. Only the red-green and white high regimes include communities changing their FD_s. The change of BS5's FD_s is stronger and consistent over the atrazine gradient (fig.3.2 C.1), compared to the change of BS4's fitness difference (fig.3.2 B.1). Hence, the gradient of atrazine affect FD_s differently based on the light regime and the population. Carroll's definition always shows the inferior competitor, thus, we cannot deduce whether the FD_s increase, decrease or stay unchanged (fig.3.2 B.2). Overall, the interaction of the combined gradients did not translate a simple addition or multiplication of their individual effects. Rather, the communities were impacted asynchronously and with an unpredictable trend. That is, based on the observation of the fig.3.2, there are no situations where we can forecast the direction or strength of the combined effect of neither $ND_{s,c}$ or $FD_{s,c}$. In conclusion, the combined effect of the gradients did not interact to mitigate their effect on the competitive outcome, rather they were, in some cases, complementary and enabled coexistence.

Finally, the definitions used imply different interpretations (fig.3.3). Carroll's definition implies a net increase of diversity among all communities except for the red-green regime. Whereas, Spaak's definition only has the blue regime with some communities under coexistence (fig3.1). For both definitions, the gradient of atrazine interacts with the light regime to increase $ND_{s,c}$. However, this increase is relatively consistent across all light regime according to Carroll's definition but not Spaak's definition. Thus, they agree on a increase of $ND_{s,c}$ and diversity but not on the strength of both increases.

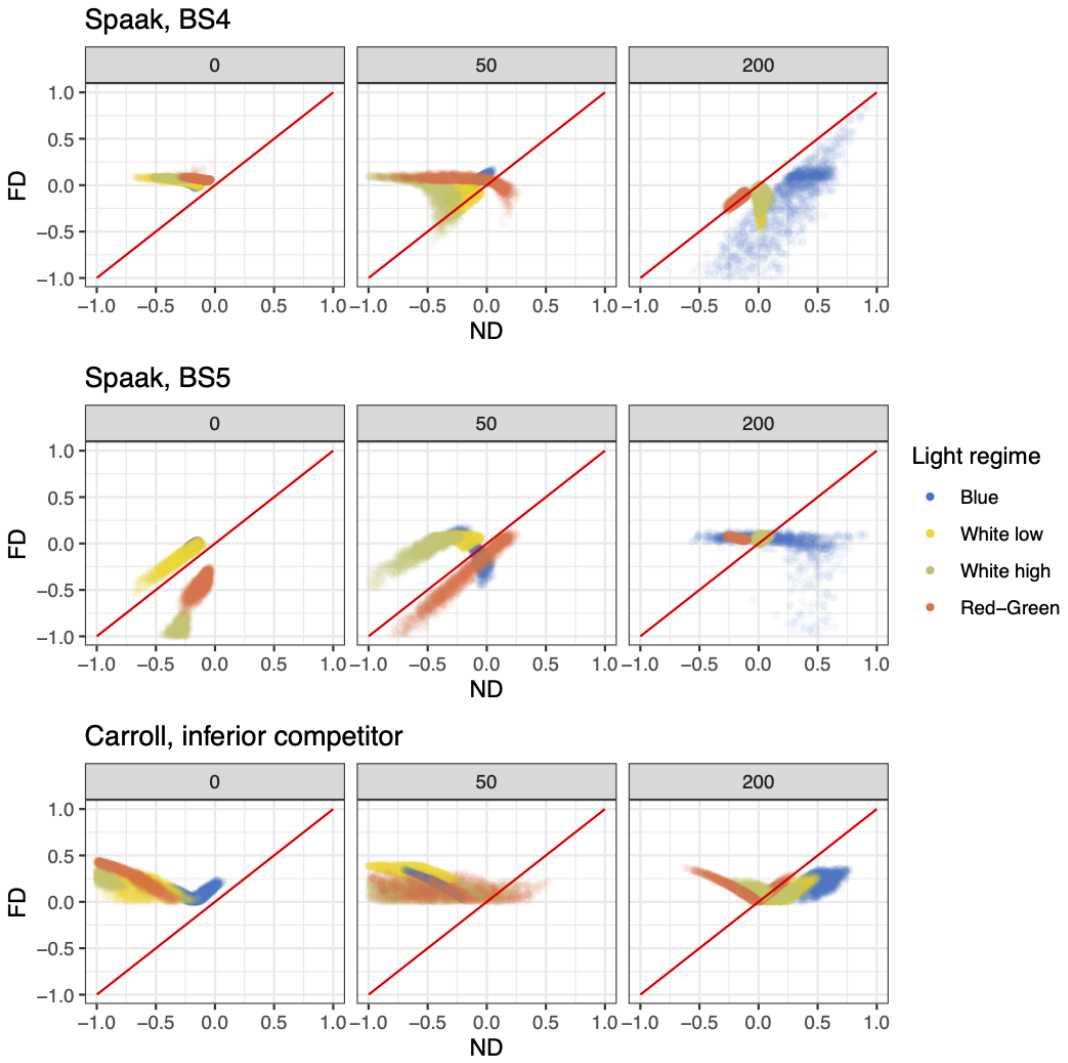

FIGURE 3.1: **The combined gradients interaction changed the outcome of competition by increasing FD_s equivalence (i.e. the difference between the FD of both competitor is reduced) and $ND_{s,c}$.** The FD_s equivalence is accompanied by a change of superior competitor: BS5's competitive strength is reduced with the increase gradient of blue light and the increase gradient of atrazine. The $ND_{s,c}$ increased, from positive to negative frequency-dependence interactions. The gradient of light regime does not induce a clear differentiation along aither $ND_{s,c}$-axis. The gradient of light regime does not mitigated the effect of the gradient of atrazine on competitive outcome, rather their individual effect are complementary and enabled an increased of diversity. FD_c always correspond to the inferior competitor, but don't allow to know its identity. In general, the experiment introduces noise. Here it is especially visible for blue light at atrazine 200 $\mu g/L$ and red-green light at atrazine 50 $\mu g/L$.

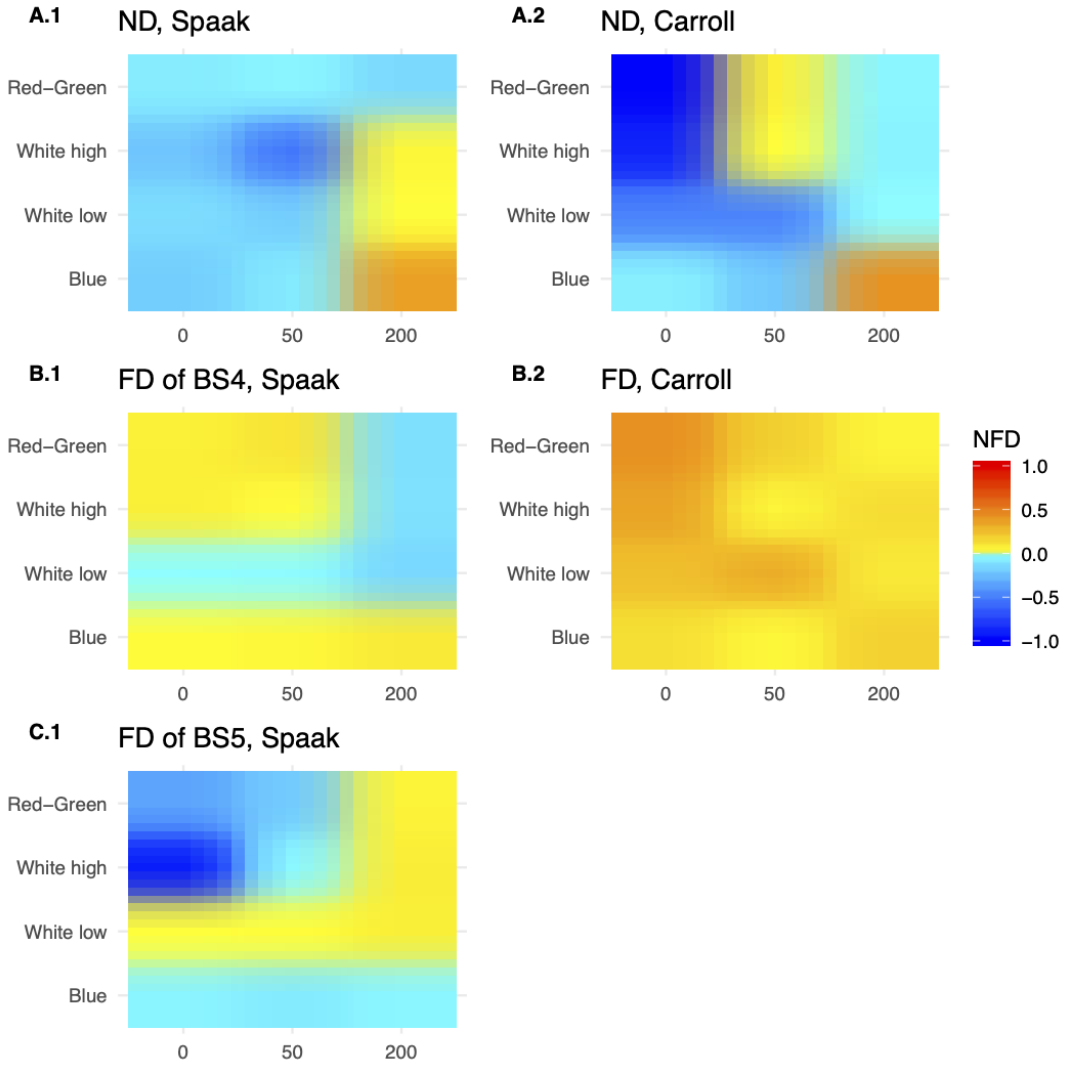

FIGURE 3.2: **The interaction of the combined gradients is complex.** If we focus on the row **A**, for the white high regime, ND_c and ND_s first decrease and then increase, hence the effect of atrazine is not monotone. However in blue light, ND_c and ND_s increase steadily, so there it's monotone. Taken together this shows that the interactions are unpredictable. The combined effect of the factors changes the superior competitor except for the blue regime (row **B** and **C**). According to Spaak's definition, the FD_s distributions have complementary trends, the increase of atrazine act positively on BS4 (i.e. increase of its competitive strenght), but negatively on BS5. However, both distributions of FD_s don't show a uniform change along the atrazine-axis. The unique FD_c don't allow us to observe this change of superior competitor (**B.2**).

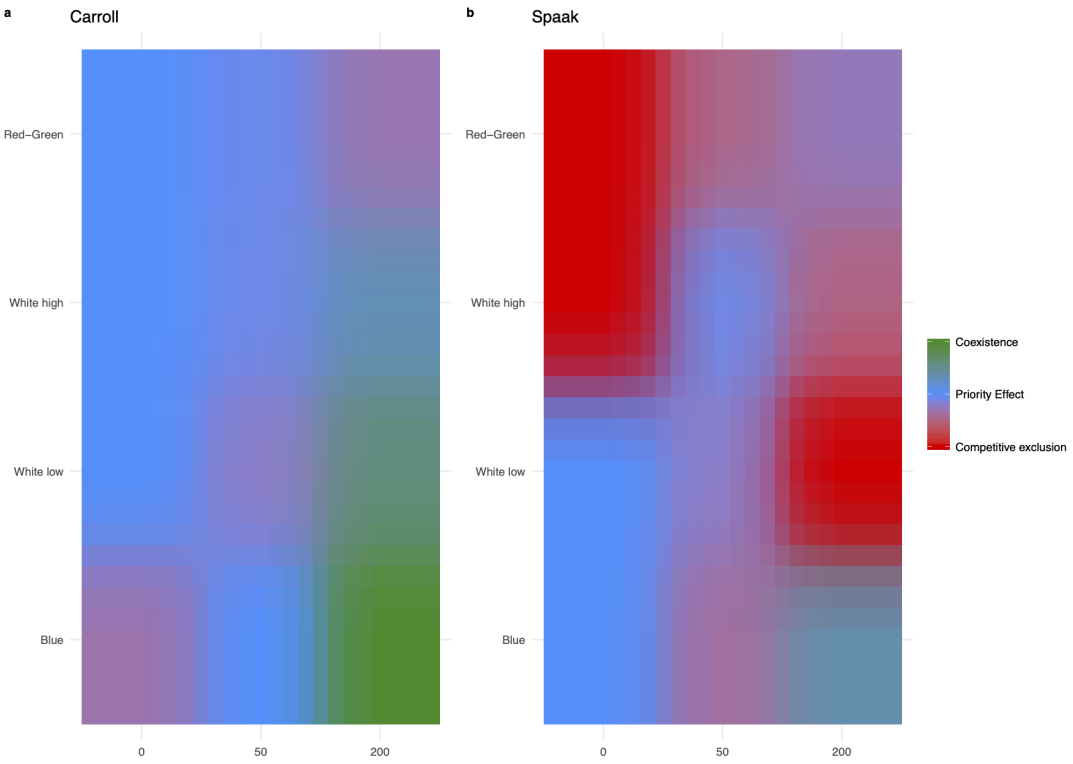

FIGURE 3.3: **The competitive outcome changed based on the definition used and along both gradients**. The colour are based on a punctuated mean of the competitive outcomes among all the communities, within each treatment.

3.2 Niche and fitness differences across systems

The distributions of $\mathcal{NFD}$ are influenced by specific interactions assembled by the biological systems' ecology. Within one definition, different interactions are observed according to the biological system studied (fig.3.4). Hence, niche and fitness differences capture the specific ecology of the communities. Communities with shorter life span (bacteria, phytoplankton and annual plant) include interactions from positive frequency dependency ($\mathcal{ND} < 0$) to negative frequency dependency ($0 < \mathcal{ND} < 1$). Only, bacteria system does not include positive frequency dependency. None of them includes mutualistic interactions ($\mathcal{ND} > 1$). Thus, when they include facilitation interactions, they are always weaker than the competing interactions. Communities with longer life span (perennial plant) include a wider range of interactions. The communities spread along the niche-axis, including three-type of interactions: mutualism, negative frequency dependency and positive frequency dependency. Thanks to Spaak's definition, we can see that mutualistic interactions ($\mathcal{ND} > 1$) always imply coexistence.

Within one biological system, the range of interactions' types are different according to the definition used (fig.3.4). Even if we expected differences in the quantitative result, within one biological system, the same biological systems should show similar spread across definitions. However, the distributions' spreads were different based on the definition used. First, Carroll's and Spaak's definitions agree that annual plant's communities are more concentrated around 0 than perennial plant. Yet, Zhao's definition shows a more concentrated distribution for perennial plant's communities. In general, Zhao's definition offers wider spread distributions. Furthermore, for one biological system, the same proportion of interactions should be present between definitions, yet, this is not the case. For instance, perennial plant communities show mutualistic interactions ($\mathcal{ND}$>1) with Spaak's definition but not according to Carroll's definition. Note that Zhao's does not allow the identification of mutuaslistic interaction based on $\mathcal{ND}$. Similarly, bacteria' communities always have negative frequency-dependence according to Carroll's and Spaak's definitions, but only include positive frequency-dependence for Zhao's definition. This discrepancy may also be due to the different papers used to computed Zhao's definition for the bacteria system. In conclusion, the spread of the distribution and the type of interactions corresponding to one biological system depend upon the definition used. Yet,

the range of $\mathcal{NFD}$ and the interactions present should only be determined by the specific ecology of the biological system.

The major determinant(s) of the competitive outcome depends upon the biological system and the definition. $\mathcal{ND}$ is consecutively identified as a determinant of coexistence. However, the importance of $\mathcal{FD}$ depends upon the biological system and the definition used (fig.3.5). Phytoplankton's and bacteria's coexisting communities have similar distribution of $\mathcal{FD}$ between coexisting and non-coexisting communities. However, bacteria's communities also share a similar $\mathcal{ND}$ according to Carroll's definition. Thus, according to Spaak's definition, both bacteria and phytoplankton system have $\mathcal{ND}$ as a determinant of competitive outcome. However, according to Carroll's definition, $\mathcal{ND}$ is not a determinant of coexistence for bacteria communities. Moreover, Zhao's definition only shows non-coexisting communities of respectively bacteria and phytoplankton systems. Thus, it does not allow a comparison between coexisting and non-coexisting communities. Annual plant and perennial plant communities respectively have similar $\mathcal{ND}$ distributions across definitions. According to Spaak's and Zhao's definitions, theirs coexisting communities include $\mathcal{ND}$ higher than 1, which in the case of Spaak's definition, translated the presence of mutualistic interactions. However, mutualistic interactions are present in half of the perennial plant whereas they only involve a small portion of annual plant communities. The ecology of perennial plant is, hence, more centred around mutualistic interactions than annual plant's ecology. The $\mathcal{FD}$ of perennial and annual plant communities are significantly smaller for coexisting communities according to Carroll's and Spaak's definitions. Thus, according to them, annual plant and perennial plant communities need both a high $\mathcal{ND}$ and a small $\mathcal{FD}$ in order to coexist. However, Zhao's definition only shows the importance of a high $\mathcal{ND}$. Overall, $\mathcal{ND}$ is the main determinant of competitive outcome across biological system. However, $\mathcal{FD}$'s importance depend upon the biological system and definition: important for annual and perennial plant systems according to Carroll's and Spaak's definition, but not the determinant of the competitive outcome for bacteria and phytoplankton systems and for communities under Zhao's definition.

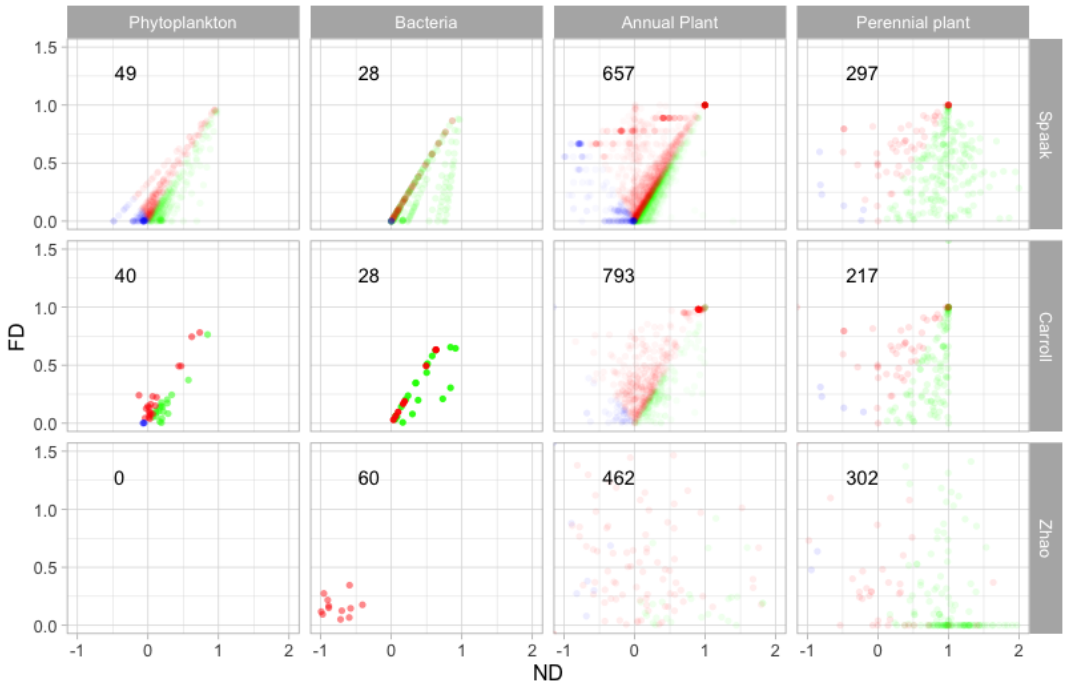

FIGURE 3.4: $\mathcal{NFD}$ **depends upon the biological system (columns) and the definition used (rows).** The different systems include different interactions. All system includes negative and positive frequency-dependence (positive and negative $\mathcal{ND}$ values), except bacteria which exclude positive frequency-dependence. Perennial plant is the only system with mutualistic interactions ($\mathcal{ND} > 1$), which is visible thanks to Spaak. The definitions associated different interactions and comparisons. For instance, both Spaak and Carroll agree on the more important accumulation of annual plant communities around 0 compared to perennial plant, Zhao does not confirm this comparison. Also, the bacteria under Zhao's definition only shows positive frequency-dependence, which are not present according to Carroll and Spaak. In general Spaak's and Carroll's definitions only differ in the incorporation of mutualism. However, they both differ from Zhao's, who tends to have wider spread distributions. It is important to note that the showed $\mathcal{FD}$corresponds to the $\mathcal{FD}$ of the inferior species, therefore $\mathcal{FD}$ is always bigger than 0. Coexisting communities are green, communities under respectively priority effect and competitive exclusion are blue and red. The shading is based on the quantity of data per graph to ensure the same amount of colour per graph. The number of communities is indicated for each graph.

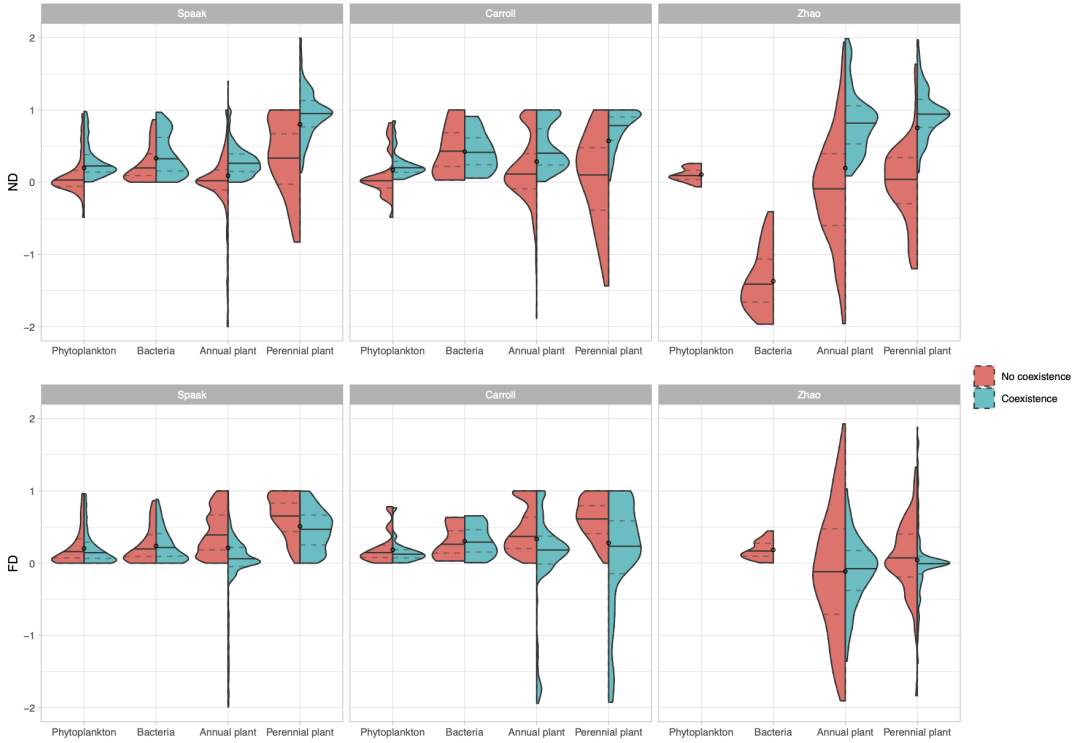

FIGURE 3.5: **Niche difference is consecutively identify as the determinant of coexistence and fitness difference's importance depends upon the biological systems and the definition.** All biological systems, have bigger $\mathcal{ND}$ for their coexisting communities except for bacteria according to Carroll's definition. However, only bacteria and phytoplankton communities present similar $\mathcal{FD}$ between their coexisting and non-coexisting communities. Annual plant and perennial plant non-coexisting communities have bigger $\mathcal{FD}$ according to both Spaak's and Carroll's definition. According to Zhao's definition, the distributions of coexisting and non-coexisting communities are similar. The definitions don't agree on the important of $\mathcal{FD}$ in determining the outcome of competition for annual and perennial plant communities. The median is indicated by the full line and the dashed lines indicate the 25 and 75 quartiles of the distribution. The black circle shows the mean of both coexisting and non-coexisting communities within one biological system.

Chapter 4

Discussion

Niche and fitness differences are driven by ELF and species ecology. ELF interact with each other, influencing the species interactions within the community. Here, these interactions between ELF had unpredictable effects, however, overall, the combined gradients resulted in increased biodiversity, due to increasing fitness equivalence and niche difference. Moreover, species ecology involves a specific range of interactions and determinant(s) of competition. In all biological systems, except bacteria according to Carroll's definition, niche difference was the determinant of competitive outcomes. The importance of fitness difference depends on the biological system. It is worth noting, however, that the respective influences of ELF and species ecology on niche and fitness differences depend on the definition used.

ELF and species ecology also interact to determine niche and fitness differences. For instance, in our experiments, the change of light regime did not affect $\mathcal{ND}$ as expected, likely due to the interactions between the ELF gradients and species ecology. Phytoplankton community structure depends on trade-offs involving key functional traits, such as light and nutrient uptake and use, interactions with natural enemies, morphological variation, temperature sensitivity, and modes of reproduction (Litchman and Klausmeier, 2008). These trad-offs have considerable impacts on intra- and interspecific competition. However, our experiment removed the need for these trade-offs: there was no grazer, optimal temperature, no light fluctuation, regular nutrient input. Thus, competitive interactions were less impacted by the homogenisation of the environment. Similarly, other experiments involving phytoplankton grown in a controlled environment are also represented by a concentrated niche difference distribution (Phytoplankton system in 3.4). Moreover, the identity of the population defines the possible competitive interactions along environmental gradients. Indeed, even across

different environment, the range of interactions are restricted at a system-level, e.g. only perennial plant's communities include mutualistic interactions, bacteria's communities do not include positive frequency-dependence interactions, phytoplankton's communities have mainly small negative frequency dependency. Also, within a biological system, the difference in ecology between its species is linked to specific functional traits determined by specific ELF. Within phytoplankton, we can discriminate functional groups based on the light-acquisition traits. For instance, diatoms, dinoflagellates, and cyanobacteria have an efficient utilisation of low light (i.e. a high efficiency of utilizing light for growth) compared to green algae, which are, however, less susceptible to photoinhibition (Litchman and Klausmeier, 2008; Schwaderer et al., 2011). Hence, cyanobacteria are sensitive to photoinhibition, but will not be strongly impacted by low incident light. That is, under a gradient of low light, the competitive interactions between cyanobacteria species should not be notably impacted. The impact of the gradient in both light spectrum and intensity was, hence, offset by the favourable controlled environment and the specific ecology of cyanobacteria (e.g. always small negative frequency-dependence interactions under controlled environment and efficient utilisation of low light).

In conclusion, niche and fitness differences are driven by the interaction of the species ecology and its ELF. The species ecology studied and its ELF will influence the answer to an ecological question. In our case, phytoplankton may not have been the most suitable biological system to study the possible mitigation of an external gradient by environmental heterogeneity, in a controlled environment. Annual plant system may have been a better system to study, as it has a wider range of interactions type, both niche and fitness differences are determinant of coexistence and field experiments are easier to set up. Understanding of the limits imposed by species ecology and the ELF on the possible species interactions found within the system needs to be enhanced to improve understanding of the mechanisms which promote biodiversity (Wainwright et al., 2016).

4.0.1 Niche and fitness differences across environmental gradients

Changes in ELF intensity or/and type affect community interactions, which impact biodiversity. Interactions between gradients of ELF impact the competitive hierarchy.

We observed that the red species (BS5) is more sensitive to changes in the light regime and increasing concentrations of atrazine than the green species (BS4). Indeed, BS5 was the superior competitor in the absence of atrazine, but was outcompeted by BS4 in high atrazine concentrations. Similarly, BS5 populations had reduced competitive strength when the light resource was homogenised. The higher sensitivity of BS5 to changes in both the light regime and atrazine concentration may be due to a net difference in interspecific functional traits. Other studies, focusing on annual plants, confirmed the increased equivalence in $\mathcal{FD}$ due to environmental changes (Wainwright et al., 2016; Perez-Ramos et al., 2019; Matias et al., 2018). Perez-Ramos et al. (2019) attributed the shift in the species competitive abilities to interspecific differences in the degree of phenotypic plasticity. Similarly, Cardinaux, Hart, and Alexander (2018) observed a change of the competitive hierarchy due to a change in a internal factor only when the characteristic of the functional trait involved with this internal factor differ between the population. Matias et al. (2018) found that, along with a reduction in average $\mathcal{FD}$, an extreme climactic change also reduces $\mathcal{ND}$, decreasing the likelihood of coexistence. Our experiment, however, demonstrated the opposite effect. The $\mathcal{ND}$ increased, which we attributed to the increased importance of negative intraspecific competition, relative to the interspecific competition. The importance of intraspecific competition may have been impacted by the sensibility of BS5. Indeed, the increased intraspecific competition within the BS4 population reduced the intensity of interspecific competition for BS5, which may have ameliorated the effect of the changing conditions for the latter species, allowing it to flourish. The stress induced by the changes of internal and external factors may have triggered the increase of facilitation interactions between the species (McIntyre, Liermann, and Revenga, 2016; Wainwright et al., 2016). That is, $\mathcal{ND}$ of the community increased, due to the greater importance of negative intraspecific competition, relative to the interspecific competition. Indeed, frequency-dependence interactions changed from positive toward negative. Overall, the differential response toward change(s) in

internal and/or external factors can be attributed to their specific ecology, which makes their inter- and/or intraspecific coefficient of competition more or less sensitive to the change(s) (Cardinaux, Hart, and Alexander, 2018). In cases where these changes favour the weaker competitor, reducing the impact of interspecific competition, relative to intraspecific competition, coexistence will be enhanced (Wainwright et al., 2016). However, indirect impacts of changes in ELF, mediated by competition, may lead to unexpected effects on ecological communities (Napier, Mordecai, and Heckman, 2016).

Changes in interactions within the community impact the outcome of competition. The competitive outcomes changed for all communities along the atrazine gradient. The direction and strength of the changes depends upon the light regime and the definition used. The changes in light regimes involved specific changes in the community's interactions. For example, changing to the most heterogeneous environment (red-green regime) does not generally cause an increase in $\mathcal{ND}$, therefore competing species in this environment cannot coexist. The heterogeneous light regime was capable of mitigating the effect of atrazine exposure. Moreover, both definitions demonstrated improved coexistence over an increasing gradient of atrazine exposure. However, under changing light regimes, coexistence varies depending on the mathematical definition of $\mathcal{NFD}$ used. Only under the blue light regime, do communities coexist according to both definitions, however the number of coexisting communities differs. The influence of the community' interactions on the outcome of competition depends on the light regime and the definition used.

The interaction between the light and atrazine gradients on $\mathcal{ND}$ and $\mathcal{FD}$ were neither monotone nor linear, but complex. Indeed, we could not, for a given treatment, predict, with any certainty, how the increase of atrazine or the increase of blue light would affect either $\mathcal{ND}$ or $\mathcal{FD}$. In nature, interactions between multiple environmental factors are even harder to predict, requiring extensive factorial experimental setups. Understanding how the interactions between these environmental factors influence interactions within communities is essential to limit future loss of biodiversity.

In conclusion, the experiments demonstrate two main points: first, that the effect of an internal factor on the community's interactions depends on the sensitivity of the species; second, that an internal factor can influence the effect of an external factor, although the direction and strength of the influence are difficult to predict. Changes in ELF affect different interactions based on the nature (i.e internal and/or external factors) and degree of change. Empirical studies have shown that perturbations in an external (Wainwright et al., 2018; Bimler et al., 2018; Matias et al., 2018; Lanuza, Bartomeus, and Godoy, 2018) or internal (Southon et al., 2013; Lanuza, Bartomeus, and Godoy, 2018; Petry et al., 2018; Germain, Mayfield, and Gilbert, 2018) factor impacts the outcome of competition by altering the competitive interactions (Usinowicz and Levine, 2018). However, in natural communities, both type of factors are perturbed by anthropogenic activities. To our knowledge, only Lanuza, Bartomeus, and Godoy (2018) and Napier, Mordecai, and Heckman (2016) considered both the influence of an external and internal factors on species interactions. Both found that the individual effect of the factors induced opposite effects on species interactions. Their combined effects, however, induced increased biodiversity, when considering spatial (Lanuza, Bartomeus, and Godoy, 2018) and temporal (Napier, Mordecai, and Heckman, 2016) heterogeneity. Indeed, Napier, Mordecai, and Heckman (2016) demonstrated that, when species have differential responses to an external factor (drought) and an internal factor (simulated herbivory), stable environments may promote competitive exclusion, while fluctuating environments may promote coexistence. Furthermore, changes in environment heterogeneity also directly affect survival and fecundity (Cadotte and Tucker, 2017; Matias et al., 2018). Thus, the specific (in)direct species responses to spatial and temporal variations of ELF should be considered when investigating the consequence of climate change or anthropogenic activities (Silvertown, 2004; Chu and Adler, 2015; Napier, Mordecai, and Heckman, 2016).

4.0.2 Niche and fitness differences across biological systems

Species ecology implies specific interactions, promoting different competitive outcomes. Based on the meta-analysis, it is not possible to determine the traits responsible for these specific interactions. However, based on the literature, we can venture some hypothesis. First, phytoplankton has the most concentrated $\mathcal{NFD}$. In the scope of the meta-analysis, the phytoplankton system is represented exclusively by freshwater green algae grown in a relatively homogeneous environment (Narwani et al., 2013; Venail et al., 2014). Being grown in a controlled environment may explain the reduced range of interaction type, in comparison to systems studied in their natural environment, such as perennial and annual plants. The major functional traits determining competitive ability and niche differentiation in phytoplankton are light utilisation traits, surface area to volume ratios, nutrient uptake and usage, interactions with natural enemies, morphological variation, temperature sensitivity, and modes of reproduction (Litchman and Klausmeier, 2008; Schwaderer et al., 2011). These major ecological axes need to be considered individually but also in combination with each other (Litchman and Klausmeier, 2008; Gallego, Venail, and Ibelings, 2019). However, here the relatively homogeneous environments did not provide the potential niche opportunities along these ecological axes. Hence, their competitive interactions are captured by small $\mathcal{NFD}$. Similarly, the bacteria system is represented by populations grown in controlled environments. Both the results of Tan, Yang, and Jiang (2017) and Li Shao-peng et al. (2019) do not show positive frequency-dependence and mutualistic interactions (illustrated by Carroll's and Spaak's definition). On the other hand, Zhao's definition actually shows positive frequency interactions. However, his communities are only composed of strains of *E.coli*, a species not present in Carroll's and Spaak's distributions. In order to explain these observations, functional traits, such as those involved in resource uptake or traits enabling to take profit from higher population density, need to be investigated in light of niche and fitness differences (Li Shao-peng et al., 2019).

Annual plants and perennial plant have a large range of interaction types. They are represented by 36 studies, in different environments, both natural (70%) and experimental (30%), which provides a greater understanding of the actual interactions found in these systems. Half coexisting communities of perennial plant include mutualistic interactions, which is the main difference with the annual plant system. Identifying the traits responsible for

this difference is not possible here, moreover, as Kraft, Godoy, and Levine (2015) have shown, consideration of combinations of traits is necessary to determine the $\mathcal{NFD}$. However, we can suppose that in general, the larger life span of perennial plant compared to the other three systems may enable the interspecific interactions and the intraspecific interactions to be both positive. Thanks to their longer life span, perennial plants would develop specific functional traits which enable interspecific and intraspecific facilitation. Therefore, this inter-system comparison of $\mathcal{NFD}$ has laid the groundwork to enhance trait-based community ecology, which may improve the understanding of competitive interactions.

Species coexistence depends upon niche difference. We found that coexisting communities always had a higher $\mathcal{ND}$ than non-coexisting communities. This finding corresponds with published experimental work (Levine and HilleRisLambers, 2009; Adler, Ellner, and Levine, 2010; Narwani et al., 2013), and thus counteract the neutral hypothesis: fitness difference and niche difference don't exist or are very small. The importance of $\mathcal{FD}$ depends upon the biological system. Bacteria and phytoplankton showed a relatively similar $\mathcal{FD}$ between coexisting and non-coexisting communities, across definitions. Perennial and annual plant's coexisting communities, however, had lower $\mathcal{FD}$. Narwani et al. (2013) and Adler, Ellner, and Levine (2010) respectively confirmed the higher importance of niche difference for coexistence for phytoplankton and perennial plant systems. Perennial plant communities present a small $\mathcal{FD}$ which would take centuries to result in the exclusion of a species even in the absence of niche difference (Adler, Ellner, and Levine, 2010). In comparison, annual plant communities present a $\mathcal{FD}$ which would take about 15 years to result in the exclusion of a species even in the absence of niche difference (Levine and HilleRisLambers, 2009). The fitness difference of annual plant species is thus more important in determining the outcome of coexistence than for the three other biological system studied here. However, in the scope of this work, it is not possible to determine the cause of this inter-system difference. Additionally, in the perrenial plant system, mutualistic interactions are of great importance. Other biological systems, not studied here, may also possess specific interaction required for coexistence, or may demonstrate an equal importance of fitness and differences. The competitive interactions of other biological systems, however, are relatively poorly studied.

Therefore, environmental variations will vary in importance, depending on species identity and the specific functional traits of that species (Snyder, 2008; Germain, Mayfield, and Gilbert, 2018; Wainwright et al., 2018; Matias et al., 2018). Species ecology encompasses both inter- and intraspecific trait differences. Interspecific trait differences define how populations interact with each other and whether it is their niche or fitness difference which is the condition for coexistence. Thanks to our inter-system comparison, we can now lay down some generalities for the four systems here (e.g. perennial plant coexisting communities need higher $\mathcal{ND}$, slightly smaller $\mathcal{FD}$ and are promoted by mutualistic interactions). However, this inter-system comparison needs to be widened to include more systems and environments. While perennial and annual plant communities were examined in a great range of environments, bacteria and phytoplankton communities were mainly studied within controlled environments. This lack of representation of natural communities prevents a comprehensive understanding of the interactions present, as well as the importance of niche and fitness differences for these systems. Interactions should, therefore, be studied in a wider range of systems and environments. Furthermore, increasing intraspecific trait variation improves the resistance of a population to environmental variations, as different individuals are able to adopt different responses (Clark, 2010; Hart, Usinowicz, and Levine, 2017). Thus the traits affected by the environmental change(s) and the intraspecific variation of these traits need to be included in the evaluation of the effect of environmental perturbation(s) on competitive outcome. Therefore, the species identities in a competing community matter. To better understand the interactions resulting from inter- and intraspecific trait variations would offer the opportunity to efficiently plan the focus of management strategies with regards to the species concerned. However, given the large number of species on the planet, being able to generalize community responses to global change at the level of biological system, or even functional group, would already be an important step forward.

4.1 The future focus of modern coexistence theory

Struggle for Existence, a call for trait-based approach

Darwin's "*Struggle for Existence*"(Darwin, 1859) regroup the two main axes discussed here: ELF and species ecology. Resource limitation and the state of the environment (as stated by Darwin) are both based on environmental heterogeneity. Moreover, interactions within and between guilds rely on the species ecology.

Nowadays, human impacts affects all four axes of *Struggle for Existence*. ELF increasingly fluctuate with environmental changes such as extreme climactic events, pollution, habitat destruction and fragmentation, invasive species introduction, etc. (Matias et al., 2018). Therefore, when investigating the influence of environmental variations on biodiversity, both the changes in ELF and the identity of the affected species should be considered (fig.1.2) (Snyder, 2008; Freckleton and Watkinson, 2001). Changing the environmental conditions will have idiosyncratic effects on species based on the related traits, affecting their coexistence (Choler, Michalet, and Callaway, 2001; Matias et al., 2018; Germain, Mayfield, and Gilbert, 2018). The lack of empirical work showing the interaction between environmental variations and the related functional traits reduce the ability to anticipate the negatives consequences of human activities on competing interactions and how to mitigate them. However, this lack of empirical work calls for the adoption of an efficient approach, considering the functional traits, the environmental gradients, the species interactions, and performance currencies: the traits-based approach (Litchman and Klausmeier, 2008). Empirical work using this approach has proven its effectiveness. Godoy and Levine (2014) look into how an invasive species may competitively exclude a native species of the same biological system, due to a difference in phenology. The native annual plant studied was disfavoured by their earlier phenology compared to the late phenology of the invader population. However, to fully explain the invasion success of the exotic population, further functional traits, and their interactions, would need to be considered. Indeed, functional traits are often in trade-off. There is often a trade-off between different functional traits, and it is these trade-offs, more than individual traits, that are capable of describing the competitive interactions (Godoy and Levine, 2014; Kraft, Godoy, and Levine, 2015; Gallego, Venail, and Ibelings, 2019).

Furthermore, the interactions of traits need to be considered alongside environment heterogeneity. Spatial and temporal environmental heterogeneity involve different response among species (Godoy and Levine, 2014; Napier, Mordecai, and Heckman, 2016). It determines the ELF in a given environment. ELF impacts species both directly (i.e. on their survival and fecundity) and indirectly (i.e. by competing interaction) (Cadotte and Tucker, 2017; Wainwright et al., 2019). Both effects involve a specific combination of functional traits.

Therefore, a trait-based approach considered the combination of functional traits and the in(direct) influence of the ELF on it, in order to obtain a complete understanding of the competitive interactions promoting the current community composition. A trait-based approach, in the light of modern coexistence theory, holds the potential to improve our understanding of community structure, and to help forecast the impact of global change.

The importance of trait's evolution

Traits are evolving in time and space. It is important to consider the reaction of niche and fitness differences to changes in traits (Litchman and Klausmeier, 2008; Petry et al., 2018; Gallego, Venail, and Ibelings, 2019; Perez-Ramos et al., 2019). When traits evolve, niche and fitness differences are affected (Zhao, Zhang, and Zhang, 2016), potentially creating opposing pressures on coexistence (Narwani et al., 2013). The inter- and intraspecific trait differences, the vital rates (Conti et al., 2018) and the differences of phenotypic plasticity (Litchman and Klausmeier, 2008; Perez-Ramos et al., 2019) are important to understand community dynamics across spatially and temporally heterogeneous environments.

Phenotypic plasticity responds to environment and competition (Conti et al., 2018). The environment is a selective force usually conferring specific traits on species surviving at a given location (Kraft et al., 2015). Nevertheless, competition can also influence the expression of traits. Under the pressure of competition and environment, traits may either converge by the selection of competitively dominance phenotypes or diverge due to the upholding of diversity in traits (Maire et al., 2012; Kraft et al., 2015). Therefore, a shift of ecologically relevant traits may lead towards either competitive exclusion, by increasing fitness difference, or promote coexistence, by increasing $\mathcal{ND}$

(Narwani et al., 2013). Overall, the effect of phenotypic plasticity on competition is determined by the interspecific differences between the populations' ability to modify their phenotypes in response to environmental heterogeneity and competition.

Evolution also plays a role in coexistence theory: whether two species have evolved by allopatry (i.e evolution in different geographical locations) or sympatry (i.e evolution in a common geographical location) changes the influence of phylogeny on niche difference (Germain, Weir, and Gilbert, 2016). As shown by Germain, Weir, and Gilbert (2016), in the case of sympatric evolution, both niche and fitness difference increase with phylogenetic distance. Whereas allopatric evolution includes a diminution of coexistence due to an increase in fitness difference and fluctuations of $\mathcal{ND}$ with phylogenetic distance. Thus, past colonisation history needs to be considered and further evaluated (Germain, Weir, and Gilbert, 2016; Tan, Yang, and Jiang, 2017).

Past and rapid evolution are therefore key influence on niche and fitness differences. It is not surprising that both the ecology and evolution of a system need to be considered to understand the dynamics of present and future competition. Indeed, in parallel to modern coexistence theory, the field of eco-evolutionary dynamics has emerged and developed since the start of the century (Hendry et al., 2011). The need to understand the eco-evolutionary dynamics captured by niche and fitness differences is essential to evaluate the drivers of competition outcomes and thus diversity.

Higher order and multispecies interactions

To fully understand the dynamics of coexistence, the need to integrate multiple species interactions alongside higher-order interactions has recently been identified (Adler et al., 2018; Lanuza, Bartomeus, and Godoy, 2018). Even if multiple species interactions have been part of the discussion for some time (Chesson, 2000; Carroll, Cardinale, and Nisbet, 2011), empirical studies have been restricted to pairwise competition. Only recent works have begun to use a structural approach for studying multispecies systems (Saavedra et al., 2017; Petry et al., 2018). This framework is critical to incorporate density-dependent interactions as well as models like rock-paper-scissors (Grilli et al., 2017). Furthermore, it is important to incorporate higher order effects. Higher order effects occur when an outsider population perturbs a pairwise competition by changing the per capita competitive interactions (Lanuza,

Bartomeus, and Godoy, 2018) but also affect individual species performance (Mayfield and Levine, 2010; Saavedra et al., 2017). Hence, a third competitor can affect the dynamic of interacting species, changing the niche and fitness differences and consequently the outcome of competition.

Until now, modern coexistence theory has been restricted to species pairs of the same guild and the effect of abiotic factors on their interactions (Godoy et al., 2018; Bartomeus and Godoy, 2018; Lanuza, Bartomeus, and Godoy, 2018). Extending the theory outside these restrictions gives the opportunity to consider key density-dependent interactions, including consumption, floral visitation, pathogenicity, parasitism, and others (Saavedra et al., 2017; Bartomeus and Godoy, 2018; Godoy et al., 2018; Petry et al., 2018). Indeed, at the present time multitrophic interactions have been included in studies as stress factors (i.e. indirect effects), decreasing or increasing niche and fitness differences between two competitors (Godoy et al., 2018; Lanuza, Bartomeus, and Godoy, 2018; Petry et al., 2018). Coexistence theory needs to integrate multitrophic and multispecies interactions to fully understand the stable coexistence requirements of large communities (Saavedra et al., 2017; Grilli et al., 2017). It is essential to consider multispecies interactions, including those across different trophic levels, to devise effective conservation strategies.

Coexistence-area scale

The choice of spatial scale, when considering competitive interactions, is critical to fully integrate the mechanisms of coexistence. A neighbourhood scale may identify a ELF as an inhibitor of biodiversity, whereas it may, in fact, promote biodiversity at regional or global scale. For instance, soil heterogeneity affects global patterns, by asynchronously filtering species between environmental patches (Lanuza, Bartomeus, and Godoy, 2018). Coexistence mechanisms can operate on scales larger than the plant interaction neighbourhood to promote biodiversity but might be overlooked, if the scale is not well chosen. Hart, Usinowicz, and Levine (2017) propose the coexistence-area relationship: "a real relationship in nature that can be used to understand the determinants of the scale-dependence of diversity maintenance". The coexistence-area relationship considers the effect of demographic stochasticity, environmental variations and dispersal, on the species-area range dynamics and persistence. The incorporation of species-area range dynamics and persistence in the scope of modern coexistence theory would improve predictions of community dynamics under climate change (Usinowicz and

Levine, 2018). Moreover, a broader scale may enable the distinction between abiotic and biotic filtering: filtering due to ELF (abiotic factors) and biotic interactions, respectively. This distinction would come alongside the discrimination between traits responsible for exclusion due to environmental filtering or due to competition (Kraft et al., 2015). For example, the invasive success of an exotic species could be rightly attributed to either traits offering higher competitive abilities and traits assembling higher fitness for the abiotic environment. Therefore, a spatial scale design in light of coexistence theory would enhance efficient conservation strategies.

An approved framework

Understanding the mechanisms that support biodiversity is of great importance for the establishment of conservation strategies (Godoy and Levine, 2014), understanding biological invasion dynamics (MacDougall, Gilbert, and Levine, 2009), limiting climate change consequences (Chu and Adler, 2015; Adler et al., 2018). Overall, the understanding of species maintenance is an essential requirement to provide an applied and useful science (Hart, Usinowicz, and Levine, 2017). It is important that we work to understand the mechanisms of species maintenance, in a fashion that is inclusive to a wide range of biological systems and interactions. In contemporary literature, primary producers are the most commonly studied systems, due to the ease with which these biological systems can be translated to a model, however, these are not representative of all biological systems. A larger investigation of many biological systems would enable effective selection of the appropriate model system to address specific future research questions. Now, more systems could be studied as there are definitions with which there are no more need to use a population model: Carroll, Cardinale, and Nisbet (2011), Zhao, Zhang, and Zhang (2016), and Spaak and Laender (2018). Yet, as shown here, these three definitions don't concur completely on the competing interactions present within one biological system. Zhao's definition was not made in order to evaluate the interactions present in the system. Between the two other definitions, the interactions found by Carroll where not inclusive. The emergence and approval of one complete definition is thus essential in order to not omit important interactions.

However, the validity of niche and fitness differences has recently been called into question, particularly the invasion growth rate which is used to define some definitions (see tab.2.2). They argued that the mean growth rate

when rare is not an efficient metric to measure persistence, as it is too easily influenced by stochastic noise (Pande et al., 2019). Furthermore, most actual definitions are based on population models. Ecologists hence have to force their data into one version of this given model. This pre-defined model could be the source of discrepancy between the coexistence prediction and the observation in natural communities. Indeed, coexistence was frequently not predicted by modelling, while it was observed in nature (Godoy and Levine, 2014; Kraft, Godoy, and Levine, 2015; Wainwright et al., 2016; Matias et al., 2018; Cardinaux, Hart, and Alexander, 2018; Bimler et al., 2018). This discrepancy between observation and prediction may be solved, thanks to the future approaches such as trait-based approach c. Moreover, data-driven modelling has the potential to improve the connection between field data and theory. Community ecologists may need to enhance data-driven modelling in order to fully enable interactions within natural communities to be expressed (Hart, Usinowicz, and Levine, 2017). A new adaptive and comprehensive framework is needed to push coexistence theory from a descriptive tool towards an effective method of forecasting the effects of global change, without which we cannot hope to promote informed conservation decisions.

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Article

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Appendix A

Details of the meta-analysis

Details of the papers gathered

TABLE A.1: List of papers used in the meta-analysis, the number of communities for each paper, and the definition of niche and fitness difference used in the paper. Adler et al., 2018 introduced 22 papers (from number 1 to 22) which initially do not all compute $\mathcal{NFD}$ but compute the inter- and intraspecific competition coefficients.

Num	Paper	Number of communities	Biological system	Definition used
	Adler, Ellner, and Levine, 2010	57	Perennial plant	Chesson, 2000
2	Hartnett et al., 1993	4	Perennial plant	
3	Sheley and James, 2014	4	Perennial plant	
4	Francis and Pyke, 1996	1	Perennial plant	
5	Kubota, 1996	1	Perennial plant	
6	Rees, Grubb, and Kelly, 1996	12	Perennial plant	
7	Moloney and Chiariello, 1998	6	Perennial plant	
8	Freckleton et al., 2000	9	Perennial plant	
9	Coomes et al., 2002	3	Perennial plant	
10	Turnbull et al., 2004	21	Perennial plant	
11	Call and Nilsen, 2005	1	Perennial plant	
12	Osunkoya, Othman, and Kahar, 2005	2	Perennial plant	
13	Suter et al., 2007	10	Perennial plant	
14	Boivin et al., 2010	6	Perennial plant	

15	Farrer, Goldberg, and King, 2012	5	Perennial plant	
16	Geijzendorffer et al., 2011	45	Perennial plant	
17	Medina-Roldán, Paz-Ferreiro, and Bardgett, 2012	2	Perennial plant	
18	Kim, Underwood, and Inouye, 2013	3	Perennial plant	
19	Zarnetske et al., 2013	90	Perennial plant	
20	Collet et al., 2014	3	Perennial plant	
21	Martorell and Freckleton, 2014	13	Perennial plant	
22	Sheley and James, 2014	4	Perennial plant	
23	Veresoglou, Rillig, and Johnson, 2018	29	Annual Plant	
24	Siefert et al., 2019	12	Annual Plant	Adler, HilleRis-Lambers, and Levine, 2007
	Narwani et al., 2013	28	Phyto - plankton	Carroll, Cardinale, and Nisbet, 2011
26	Venail et al., 2014	28	Phyto - plankton	
27	Tan et al., 2016	6	Bacteria	
28	Ocampo-Ariza et al., 2018	1	Annual Plant	
29	Veresoglou, Rillig, and Johnson, 2018	408	Annual Plant	
30	Li Shao-peng et al., 2019	24	Bacteria	
	Godoy and Levine, 2014	9	Annual Plant	Godoy and Levine, 2014
32	Godoy, Kraft, and Levine, 2014	153	Annual Plant	
33	Germain, Weir, and Gilbert, 2016	40	Annual Plant	
34	Hallett et al., 2018	15	Annual Plant	

35	Rey, Manzaneda, and Alcántara, 2017	2	Annual Plant	
36	Cardinaux, Hart, and Alexander, 2018	8	Annual Plant	
37	Lanuza, Bartomeus, and Godoy, 2018	15	Annual Plant	
38	Matias et al., 2018	90	Annual Plant	
39	Petry et al., 2018	55	Annual Plant	
40	Wainwright et al., 2018	24	Annual Plant	
41	Zhao, Zhang, and Zhang, 2016	60	Bacteria	Zhao, Zhang, and Zhang, 2016
42	Bimler et al., 2018	12	Annual Plant	Bimler et al., 2018
Total		1321		

Details of the communities gathered

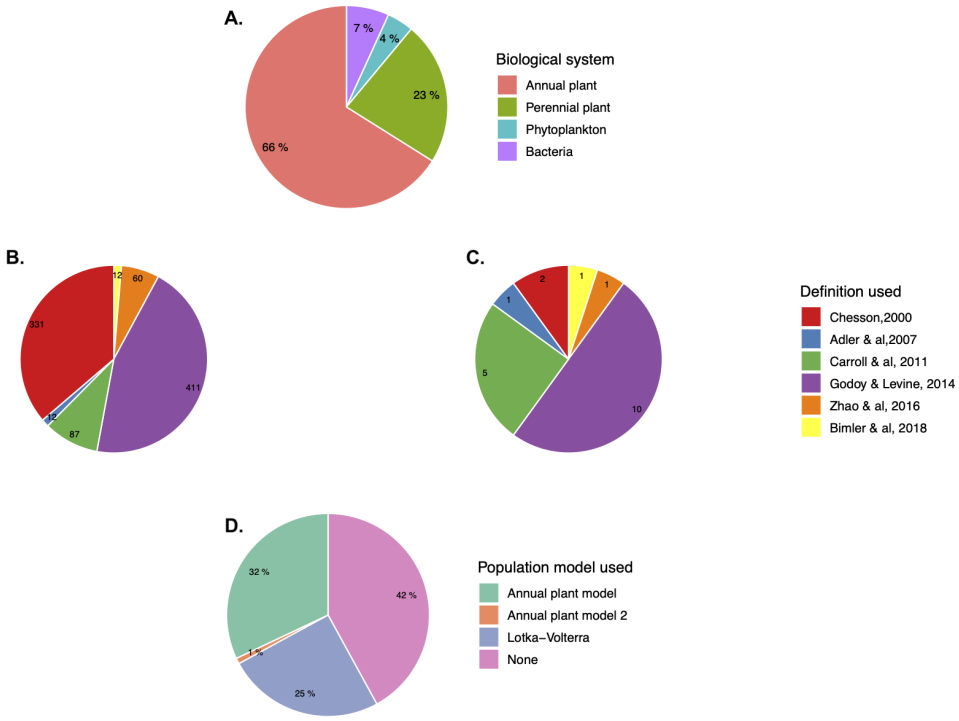

FIGURE A.1: Information of the data used. **(A)** Distribution of the 4 biological systems studied. **(B)** Number of communities per initial definitions of niche and fitness differences. **(C)** Number of papers per initial definitions of niche and fitness differences.**(D)** Distribution of the population model used (mathematical equations below). The 21 papers gathers by the meta-analysis of Adler et al. (2018) were considered as one paper.

Details of population model

Population model are used to estimate the intra- and interspecific competition coefficients based on the experimental data. The annual plant population model (Levine and HilleRisLambers, 2009), with a seed bank can be described as:

$$\frac{N_{i,t+1}}{N_{i,t}} = (1 - g_i)s_i + g_i F_i \tag{A.1}$$

With g_i and s_i respectively the seed germination rate and seed survival rate. $N_{i,t}$ is the density of species i at the time t. F_i is the per-germinant fecundity. The Annual Plant model and the second Annual Plant models can be distinguish based on the function describing F_i.

Annual Plant model (Godoy and Levine, 2014):

$$F_{i,t} = \frac{\lambda_i}{1 - a_{ii}g_iN_{i,t} - a_{ij}g_jN_{j,t}} \tag{A.2}$$

λ_i is the per-germinant fecundity in the absence of competition.
a_{ii} and a_{ij} are respectively the intraspecific and interspecific competition coefficient computed based on a Annual plant model.
The second Annual Plant model (Bimler et al., 2018):

$$F_{i,t} = \lambda_i \exp -a_{ii}g_iN_{i,t} - a_{ij}g_jN_{j,t} \tag{A.3}$$

The two-species Lotka–Volterra competition model can be described by two equations (Adler et al., 2018):

$$\frac{dN_i}{dt} = r_iN_i(1 - \alpha_{ii}N_i - \alpha_{ij}N_j) \tag{A.4}$$

$$\frac{dN_j}{dt} = r_jN_j(1 - \alpha_{jj}N_j - \alpha_{ji}N_i) \tag{A.5}$$

N_i is the density of species i and r is the intrinsic growth rate.
λ_{ij} and λ_{ji} are respectively the intraspecific and interspecific competition coefficient compute based on the Lotka-Voltera model.

The definition used in this work do not require the used of a specific population model as explained in the section 2.2.4.

Appendix B

Growth rate of the two strains of cyanobacteria over time

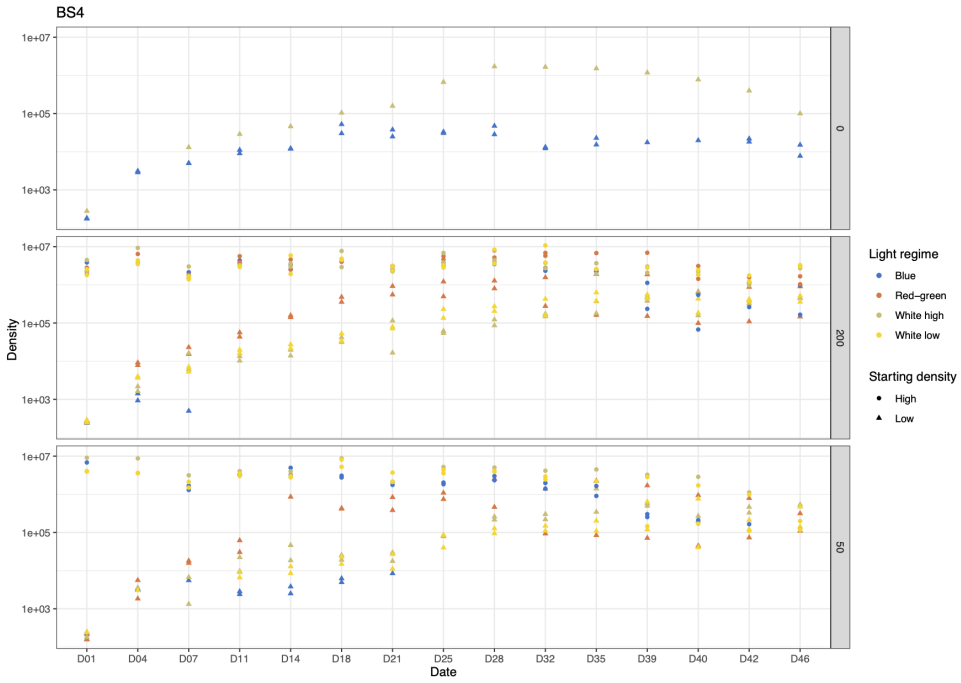

FIGURE B.1: Growth rate of BS4's cultures with two starting conditions : (i)initially low-concentration population (ii) initially high-concentration population. The cultures have reached equilibrium after about 28 days (i.e. the initially low-concentration population is of equal density to the initially high-concentration population). There are two replicates per starting condition. At 0 g/L atrazine, only the blue light and the white high regimes have viable communities.

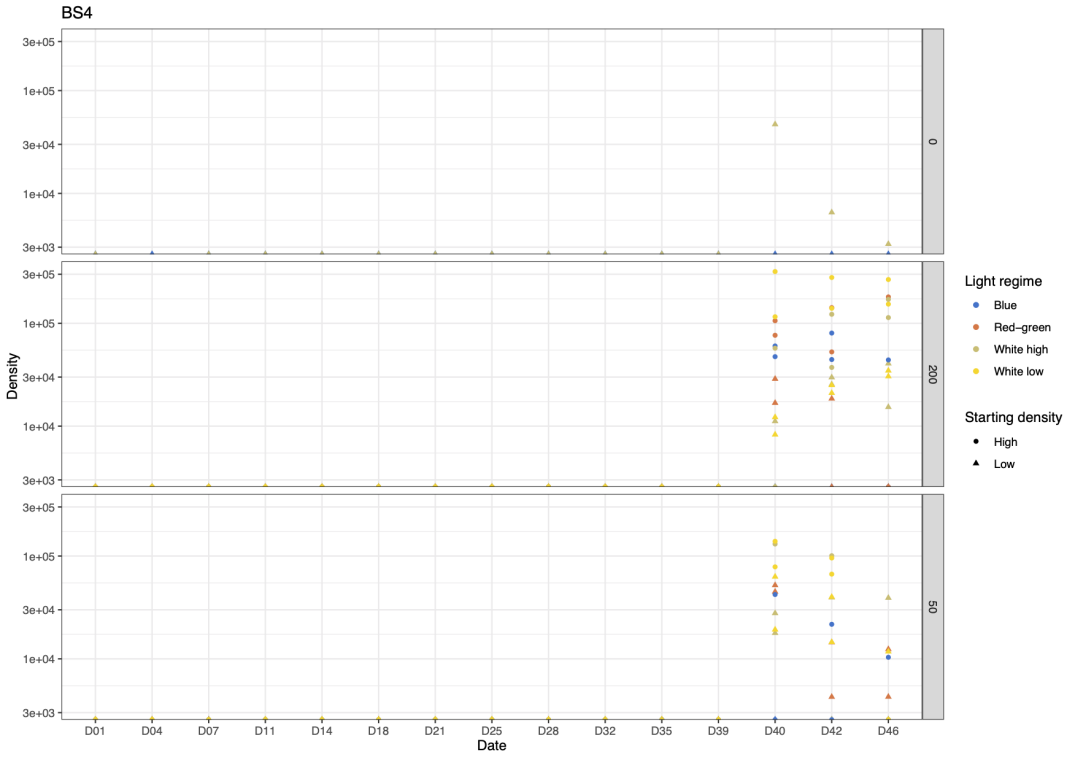

FIGURE B.2: Growth rate of BS5's population when invading BS4's cultures. The invasion is triggered when both population have reached equilibrium (i.e. the initially low-concentration population is of equal density to the initially high-concentration population). There are two replicates per communities.

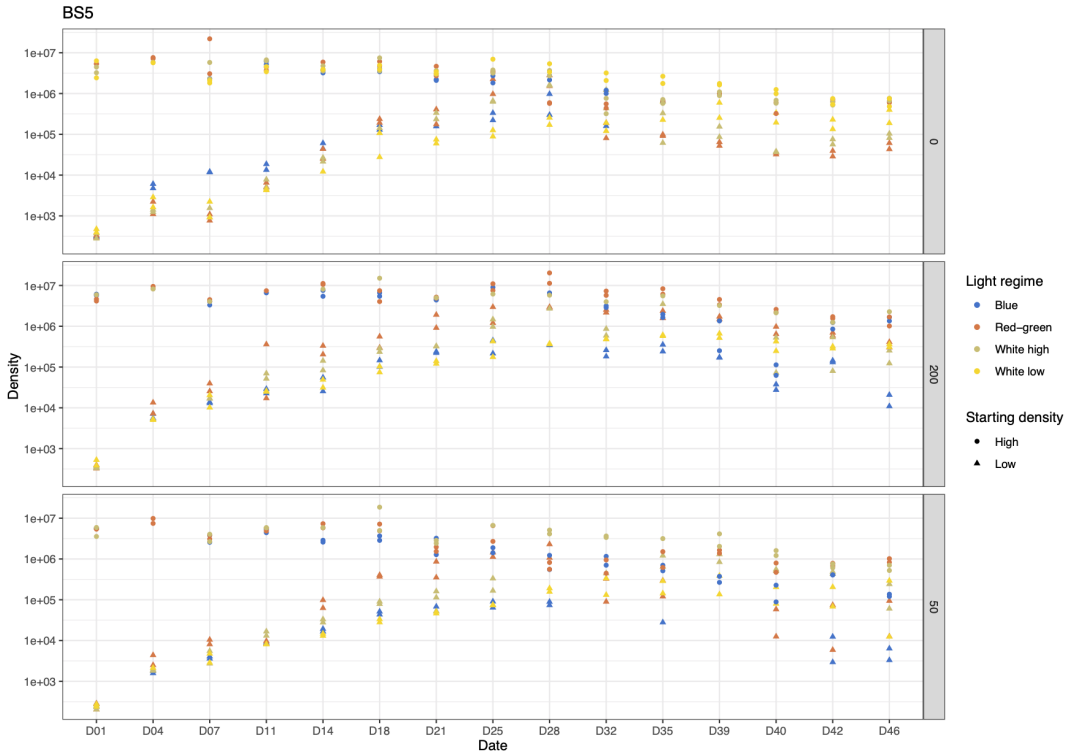

FIGURE B.3: Growth rate of BS5's cultures with two starting conditions : (i)initially low-concentration population (ii) initially high-concentration population. The cultures have reached equilibrium after about 28 days (i.e. the initially low-concentration population is of equal density to the initially high-concentration population). There are two replicates per starting condition.

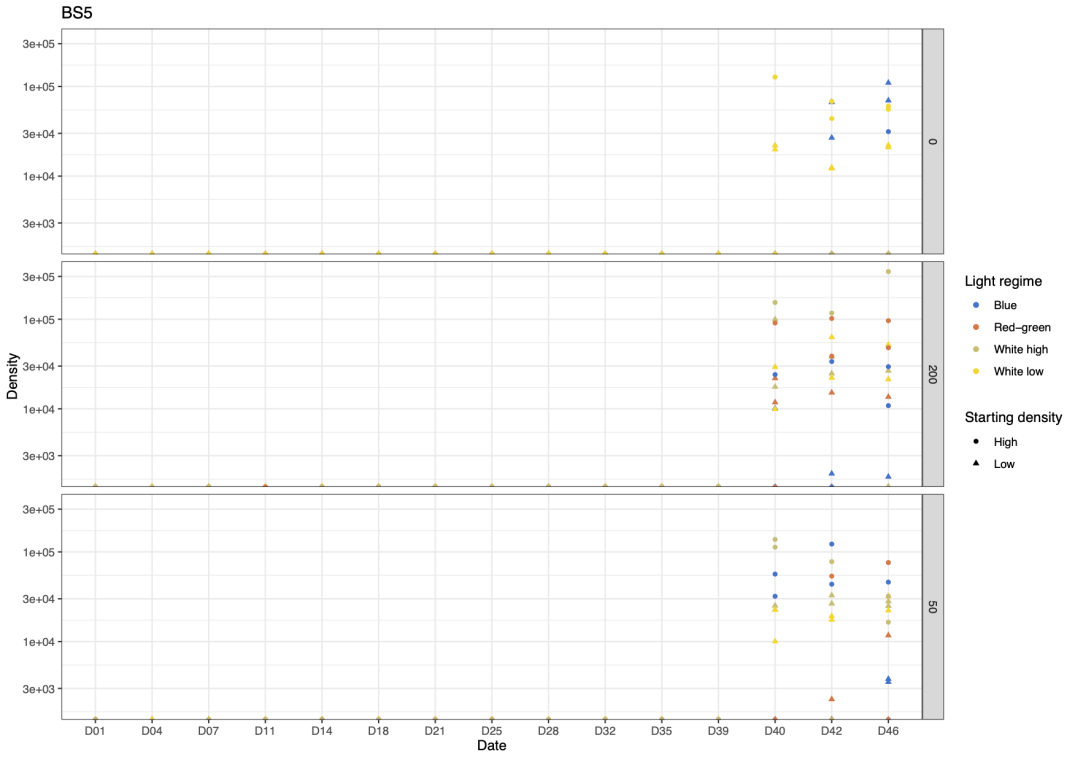

FIGURE B.4: Growth rate of BS4's population when invading BS5's cultures. The invasion is triggered when both population have reached equilibrium (i.e. the initially low-concentration population is of equal density to the initially high-concentration population). There are two replicates per communities.