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LETTER

Intuitive and broadly applicable definitions of niche and fitness differences

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Abstract

Explaining nature's biodiversity is a key challenge for science. To persist, populations must be able to grow faster when rare, a feature called negative frequency dependence and quantified as 'niche differences' ($\mathcal{N}$) in modern coexistence theory. Here, we first show that available definitions of $\mathcal{N}$ differ in how $\mathcal{N}$ link to species interactions, are difficult to interpret and often apply to specific community types only. We then present a new definition of $\mathcal{N}$ that is intuitive and applicable to a broader set of (modelled and empirical) communities than is currently the case, filling a main gap in the literature. Given $\mathcal{N}$, we also redefine fitness differences ($\mathcal{F}$) and illustrate how $\mathcal{N}$ and $\mathcal{F}$ determine coexistence. Finally, we demonstrate how to apply our definitions to theoretical models and experimental data, and provide ideas on how they can facilitate comparison and synthesis in community ecology.

Keywords

Coexistence, competition, fitness differences, multispecies, mutualism, niche differences.

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INTRODUCTION

In order to persist through time, species must exhibit frequency-dependent population growth. Natural communities host a multitude of mechanisms that can lead to frequency dependence. Well-known examples include resource partitioning (Adler *et al.* 2007; Levine & HilleRisLambers 2009), differential vulnerability to predators (Carson & Root 2000; Chesson & Kuang 2008; Allan *et al.* 2010), differential associations with mutualists (Siefert *et al.* 2018; Johnson & Bronstein 2019), phenological separation (Usinowicz *et al.* 2017) or occupation of distinct microhabitats (Silvertown 2004). These mechanisms have been collectively coined as stabilising mechanisms that increase 'niche differences' (Chesson 2000; HilleRisLambers *et al.* 2012; Letten *et al.* 2017).

In modern coexistence theory, one way of quantifying the strength of niche differences is to compare observed population growth with the population growth that is expected when niche differences would be absent (Chesson 2000, 2003; Adler *et al.* 2007, 2010). Without niche differences, one of the species will eventually exclude all others, where the rate of exclusion depends on the competitive advantage of the winner. This competitive advantage is often called 'fitness difference' (Barabás *et al.* (2018); Chesson 2000, 2003; Hart *et al.* 2018). A key question is if niche differences in natural systems are sufficiently strong to overcome fitness differences and save species from extinction (Hubell 2001; Angert *et al.* 2009; Narwani *et al.* 2013; Connolly *et al.* 2017; Harris *et al.* 2017; Usinowicz *et al.* 2017; Adler *et al.* 2018).

Niche and fitness differences formalise species persistence in a way that is phenomenological. That is, one does not need to specify the details of the community or its environment, but rather focuses on higher level processes, that is how species grow under different circumstances. This feature would in principle allow synthetic studies across different community types and environmental conditions, with niche and fitness differences acting as common currency that represent the net outcome of detailed ecological mechanisms. Such studies are important because they foster a unified understanding of community composition (Adler *et al.* 2018) and facilitate studying how environmental context and community characteristics jointly influence species persistence, which can help understanding global change effects (Grainger *et al.* 2019).

At present, however, the application of niche and fitness differences is hampered by a lack of consensus on their mathematical definition. Indeed, the operationalisation of these concepts has been discussed for almost a century and new methods are being constantly proposed (Renkonen 1938; Morisita 1959; Hurlbert 1978; Chesson 1990, 2000, 2003; Carroll *et al.* 2011; Bimler *et al.* 2018), leading to a proliferation of mathematical definitions of niche and fitness differences. We identified 10 definitions available in the literature (Appendix A) and found that every single existing definition displays a number of features that limit its applicability. For instance, most of the definitions only apply to communities whose dynamics obey a specific mathematical model (Chesson 1990; Adler *et al.* 2007; Chesson & Kuang 2008; Godoy & Levine 2014; Saavedra *et al.* 2017; Bimler *et al.* 2018). This means that the applicability of these definitions is limited to specific community types. In addition, several definitions cannot be computed for communities with positive species interactions and/or more than two species. Also, not all definitions allow inference of coexistence or exclusion, that is, niche and fitness differences do not predict whether species will persist (Appendix A). Finally, different definitions imply different ranges for niche and fitness differences. Hence, we cannot readily compare results from different authors (Godoy &

Levine 2014; Chu & Adler 2015; Grainger *et al.* 2019; Song *et al.* 2019; Appendix A).

Here, we first show that available definitions of niche differences do not align with biological intuition and present a new definition that does. We also derive the corresponding definition of fitness differences and coexistence conditions. An important feature of these new definitions is that they apply to any mathematical model or empirical system driven by any mechanism, with the sole critical requirement that invasion analysis correctly predicts coexistence. The flexibility of the new definitions allows comparing different community types, containing an arbitrary number of species and a variety of species interactions, addressing a key limitation in theoretical ecology. Finally, we illustrate theoretical and experimental applications of the new definitions. To this end, we apply the definitions to various models representing a suite of interaction types. We also show how simple growth experiments suffice to quantify niche and fitness differences, using an empirical dataset of two picocyanobacteria competing for light.

THEORY

A diversity of definitions

To facilitate interpretation and broad application, the definitions for niche and fitness differences should align with biological intuition. Intuition dictates that niche differentiation facilitates persistence ($\mathcal{N}$ increases as species persist more easily). In addition, a definition of $\mathcal{N}$ that is consistent with intuition must satisfy five constraints. First, when intra- and interspecific interactions are of equal size ($\alpha = -1$in Fig. 1), individuals of both species are interchangeable: the effect an individual has on another individual does not depend on species identity. Thus, $\mathcal{N}$ should equal 0 (black triangle in Fig. 1; Chesson 1990). Second, when interspecific interactions are absent ($\alpha = 0$ in Fig. 1), each species grows as if other species are absent. Thus, $\mathcal{N}$ should be some predefined non-zero real number that indicates complete niche differentiation, for example 1 (black dot in Fig. 1; Godoy & Levine 2014). The third point is the logical consequence of these first two points: intermediate interspecific interaction strengths should result in $\mathcal{N}$ between 0 and 1 (solid rectangle in Fig. 1). Fourth, when interspecific interactions are more negative than intraspecific interactions, persistence is 'harder' ($\mathcal{N}$ should be smaller) than if species occupied exactly the same niche ($\mathcal{N} = 0$). Consequently, $\mathcal{N}$ should be negative (dashed rectangle in Fig. 1), as has been stated before (Mordecai 2011; Ke & Letten 2018). Fifth, when interspecific interactions are positive, for example because of facilitation, the presence of other species makes persistence 'easier' ($\mathcal{N}$ should be greater) than if these other species would have no effect on the focal species (i.e. interspecific interactions are absent, in which case $\mathcal{N} = 1$). Thus, $\mathcal{N}$ should inevitably be greater than 1 (dotted rectangle in Fig. 1) when species interactions are positive.

We found that available definitions of $\mathcal{N}$ are unlikely to fulfil the five requirements outlined here. To show this, we computed $\mathcal{N}$ for the annual plant model, a workhorse of theoretical ecology (Adler *et al.* 2007, 2010, 2012; Angert *et al.* 2009; Levine & HilleRisLambers 2009; Godoy *et al.* 2014; Germain *et al.* 2016; Fig. 1), using eight of the 10 definitions for niche and fitness differences. The two other definitions cannot be applied to the annual plant model. All definitions return greater $\mathcal{N}$ as species interactions shift from strongly negative, over weakly negative, to positive. However, different definitions for niche difference imply a variety of niche difference responses to the strength and sign of species interactions (Fig. 1). In addition, these definitions do not map these species interactions to the intuitive niche difference values, as stated above (but see Chesson (1990); Chesson & Kuang (2008); Godoy & Levine (2014)). We therefore introduce, in the next section, a new definition that does align with biological intuition.

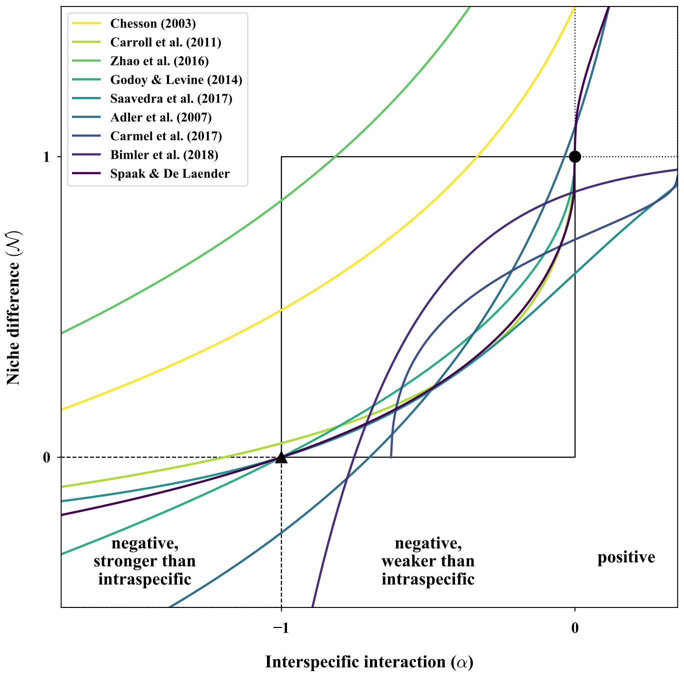

Figure 1 The modelled response of niche differences ($\mathcal{N}$) to the interspecific interaction strength α between two annual plants differs among available definitions. The black triangle indicates where inter- and intraspecific interactions are equal ($\alpha = -1$), and so species occupy the same niche, meaning that $\mathcal{N}$ should be 0. Communities with stronger interspecific interactions must have $\mathcal{N} < 0$ (dashed rectangle). The black dot indicates where species do not interact ($\alpha = 0$), and so species have completely different niches, meaning $\mathcal{N}$ should be 1. Consequently, communities in which interspecific interactions are positive ($\alpha > 0$) should have $\mathcal{N}$ larger than 1 (dotted rectangle). Finally, for all communities where $-1 \leq \alpha \leq 0$, $\mathcal{N}$ must have intermediate values ($0 \leq \mathcal{N} \leq 1$, solid rectangle). The new definition proposed here (red), which is applicable to a wide variety of models and experimental data (i.e. not only the annual plant model), complies with this biological intuition. Parameter values, a plot for the corresponding fitness differences ($\mathcal{F}$), and mathematical expressions of the $\mathcal{N}$ and $\mathcal{F}$ definitions are in Appendix A.

Defining niche differences based on biological intuition

Here, we first construct a general definition for $\mathcal{N}$ that fulfils the five requirements outlined in the previous section, and is therefore based on biological intuition. To construct a definition of $\mathcal{N}$, we start by considering the per capita growth of a species i

$$\frac{1}{N_i}\frac{dN_i}{dt} = f_i\left(N_i, N_j\right) \tag{1}$$

where N_i, N_j are densities of species i and j ($i \neq j$) with which i interacts. f_i can be essentially any function that describes the per capita growth rate of species i. A discrete system $N_i(t+1) = N_i(t)f_i\left(N_i(t), N_j(t)\right)$ can be analysed as well, by taking the natural logarithm that is $\tilde{f}_i\left(N_i, N_j\right) = \log(f_i\left(N_i, N_j\right))$ (Chesson 1994, 2003). As done mostly in modern coexistence theory (but see Schreiber *et al.* (2019)), we do not consider Allee effects (positive density dependence), such that we can assume $f_i(0,0) > f_i(N_i, 0)$: a species grows faster when its density is lower. While accounting for Allee effects is technically possible with the definitions proposed here, interpretation of $\mathcal{N}$ will be challenging (see below). Furthermore, we assume that each species has a stable monoculture equilibrium denoted N_i^* and that the invasion growth rate $f_i\left(0, N_j^*\right)$ correctly predicts coexistence. That is, the two species i and j coexist if and only if both species have a positive 'invasion growth rate' ($f_i\left(0, N_j^*\right) > 0$). The invasion growth rate is the growth rate of a species when it is reduced to low density (≈ 0) and the other species is at its monoculture equilibrium density. Examples where invasion analysis does not predict coexistence are found in Barabás *et al.* (2018) and Schreiber *et al.* (2019). We only assume a fixed point equilibrium for notational simplicity, but the definitions also apply to a stationary distribution equilibrium.

When $\mathcal{N} = 0$, inter- and intraspecific interactions are equal. Thus, the identity of the individual does not matter, such that, in eqn 1, $f_i\left(N_i, N_j\right)$ is equivalent to writing $f_i\left(N_i + N_j, 0\right)$. However, one cannot simply sum species densities. For example, a large tree and a small forb may draw down the same resource. However, they will most likely do so to a different extent. Resource consumption of each individual tree may be much greater than the resource consumption of each individual forb. Therefore, we introduce a conversion factor, c_j, that translates the density of a species into a density of the other species, that would consume the same amount of resources. No mechanistic understanding of the species interactions is necessary to compute c_j, and as we show below, it can be estimated empirically. While the ecological interpretation of c is discussed below (Applications), we already stress that these are *not* the scaling factors known from modern coexistence theory (Barabás *et al.* 2018; Chesson 1994; Ellner *et al.* 2019). Hence, the growth of species i can be written as:

$$\mathcal{N} = 0 \Rightarrow f_i\left(N_i, N_j\right) = f_i\left(N_i + c_jN_j, 0\right) \tag{2}$$

When $\mathcal{N} = 1$, interspecific species interactions are absent. Thus, species j has no effect on species i, and so species i grows as if species j were absent, that is we can put the density of j to zero:

$$\mathcal{N} = 1 \Rightarrow f_i\left(N_i, N_j\right) = f_i(N_i, 0) \tag{3}$$

Equations 1–3 hold for all densities N_i, N_j. However, we will now apply it to obtain species i's invasion growth rate, which allows interference about coexistence. This corresponds to choosing $N_i \approx 0$ and $N_j = N_j^*$, which is j's monoculture equilibrium. In this scenario, eqns 2 and 3 become $\mathcal{N} = 0 \Rightarrow f_i\left(0, N_j^*\right) = f_i\left(c_jN_j^*, 0\right)$ and $\mathcal{N} = 1 \Rightarrow f_i\left(0, N_j^*\right) = f_i(0,0)$. Here, $f_i(0,0)$ is the intrinsic growth rate and $f_i\left(0, N_j^*\right)$ is the invasion growth rate. For $f_i\left(c_jN_j^*, 0\right)$, we introduce the term no-niche growth rate of species i. This is the growth rate of species i if there was no niche differentiation, that is if $\mathcal{N}$ would be 0. Technically, the no-niche growth rate of species i is the growth rate at the converted monoculture density of its competitor (species j).

The main idea behind the new definitions is to let $\mathcal{N}$ fulfil the requirements from the previous section. The simplest way to do so is by writing $\mathcal{N}$ as a linear function that equates to 2 and 3 at the desired growth rates:

$$\mathcal{N}_i = \frac{f_i\left(0, N_j^*\right) - f_i\left(c_jN_j^*, 0\right)}{f_i(0,0) - f_i\left(c_jN_j^*, 0\right)} \tag{4}$$

This new definition by design fulfils the requirements, which can be seen when applying it to the annual plant model (Fig. 1). When species interact negatively and do so more within than between species, $\mathcal{N}_i$ is bounded in $[0, 1]$ (solid rectangle). When interspecific interactions are more negative than intraspecific interactions, species grow slower when rare ($f_i\left(0, N_j^*\right) < f_i\left(c_jN_j^*, 0\right)$) and $\mathcal{N}_i$ will be negative (dashed rectangle). When interspecific effects are positive ($f_i(0,0) < f_i\left(0, N_j^*\right)$), $\mathcal{N}_i$ is larger than 1 (dotted rectangle).

This new definition should be interpreted as follows. The numerator of $\mathcal{N}_i$ compares the growth of species i when only interspecific interactions are present ($f_i\left(0, N_j^*\right)$) with its growth when only intraspecific interactions matter ($f_i\left(c_jN_j^*, 0\right)$). Note that in this last growth rate, $c_jN_j^*$ denotes a density of species i. Both growth rates are evaluated at the same total converted density, but at different frequencies of species i, being 0% in $f_i\left(0, N_j^*\right)$ and 100% in $f_i\left(c_jN_j^*, 0\right)$.The numerator of $\mathcal{N}_i$ therefore effectively measures frequency dependence of species i (Adler *et al.* 2007; Levine & HilleRisLambers 2009). The denominator of $\mathcal{N}_i$, which is always positive and thus does not influence the sign of $\mathcal{N}_i$, compares the growth of species i when its density is ≈ 0 with its growth when the density of species i is at the converted equilibrium density of j ($c_jN_j^*$). Thus, the denominator of $\mathcal{N}_i$ measures the strength of species i's density dependence. $\mathcal{N}_i$ therefore measures the strength of frequency dependence, relative to that of density dependence. According to this new definition, and unlike almost all other definitions (but see Adler *et al.* (2007)), $\mathcal{N}_i$ is species-specific and is therefore not a community characteristic. However, $\mathcal{N}_i$ does depend on species j as well, as species j will influence species i's invasion and no-niche growth rates (eqn 4). In what follows, we use the subscript i ($\mathcal{N}_i$) only to distinguish between the niche differences of the species, and use $\mathcal{N}$ to refer to niche differences in general.

Fitness differences and coexistence

The novel definition of $\mathcal{N}$ implies a new definition of the fitness difference $\mathcal{F}$. Verbally, $\mathcal{F}$ should represent the per capita growth rate when both species occupy the same niche, that is when $\mathcal{N} = 0$ (Adler *et al.* 2010; Barabás *et al.* 2018). Therefore

$$\mathcal{F}_i = \frac{f_i\left(c_j N_j^*, 0\right)}{f_i(0,0)} \tag{5}$$

$\mathcal{F}_i$ ranges from $-\infty$ to 1 (because we assume no Allee effects, i.e. $f_i\left(c_j N_j^*, 0\right) < f_i(0,0)$) and measures how well species *i* grows in the absence of frequency dependence (no-niche growth rate, numerator; Adler *et al.* 2007, 2010), compared to its intrinsic growth rate (denominator). When $\mathcal{F}_i$ is 0, species *i* is equally competitive as species *j*. Otherwise exactly one species, the competitive dominant, has $\mathcal{F}_i > 0$.

$\mathcal{N}$ and $\mathcal{F}$ both depend on the intrinsic and the no-niche growth rate. The no-niche growth rate itself depends implicitly on the invasion growth rate as well (see below eqn 9). In general, changing any underlying parameter will affect both $\mathcal{N}$ and $\mathcal{F}$, that is. they are interdependent (Song *et al.* 2019).

Now that we have defined both $\mathcal{N}$ and $\mathcal{F}$, we can evaluate when species *i* can coexist with species *j*. Interestingly, normalising the invasion growth rate by the intrinsic growth rate yields $\frac{f_i\left(0, N_j^*\right)}{f_i(0,0)} = \mathcal{N}_i + \mathcal{F}_i - \mathcal{N}_i \cdot \mathcal{F}_i$ (Appendix B). Thus, *i* can persist within the community when[1]:

$$-\mathcal{F}_i < \frac{\mathcal{N}_i}{1 - \mathcal{N}_i} \tag{6}$$

This inequality formalises the idea that species persist, when $\mathcal{N}$ ‘overcome” $\mathcal{F}$. However, the inequality is only meaningful if invasion growth rate correctly predicts coexistence. This inequality yields a number of important insights. First, as for $\mathcal{N}$, also $\mathcal{F}$ is species specific. Taken together, this shows that the above inequality should therefore be considered as the condition for species *i* to persist. Only if all species from a community fulfil this inequality, all species will coexist. Second, the minus sign on the left-hand side of eqn 6 shows that a high $\mathcal{F}_i$ implies a competitive advantage for species *i*, which is consistent with previous insights (Chesson 2000, 2003; Adler *et al.* 2007). Third, completely different niches are sufficient to overcome arbitrarily large $\mathcal{F}_i$ (i.e. $\mathcal{N} = 1 \Rightarrow -\mathcal{F} < \frac{1}{1-1} = \infty$). Conversely, if species occupy the same niche (i.e. $\mathcal{N} = 0 \Rightarrow -\mathcal{F} < \frac{0}{1-0} = 0$), coexistence is only possible under neutrality (i.e. $\mathcal{F}_i = \mathcal{F}_j = 0$). Fourth, species with negative $\mathcal{N}$ cannot coexist, as species' growth is positively frequency dependent: species grow faster when abundant (Mordecai 2011; Ke & Letten 2018; Schreiber *et al.* 2019).

Extension beyond species pairs

The definitions for $\mathcal{N}$ and $\mathcal{F}$ naturally extend to communities composed of more than two species, hereafter ‘multispecies communities’. To show this, we generalised the invasion growth rate and the no-niche growth rate to the case of multispecies communities (for technical details, see Appendix B):

$$\mathcal{N}_i = \frac{f_i\left(0, \mathbf{N}^{-\mathbf{i},*}\right) - f_i\left(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \mathbf{0}\right)}{f_i(0, \mathbf{0}) - f_i\left(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \mathbf{0}\right)} \tag{7}$$

$$\mathcal{F}_i = \frac{f_i\left(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \mathbf{0}\right)}{f_i(0, \mathbf{0})} \tag{8}$$

Here $\mathbf{N}^{-\mathbf{i},*}$ is the vector of equilibrium densities in the absence of species *i*, **0** denotes the absence of all species other than *i*, and similar to the definition for species pairs (eqn 4), c_{ij} converts densities of species *j* into *i*. These definitions measure the net effect of species interactions on $\mathcal{N}$ and $\mathcal{F}$, that is including direct, indirect (Godoy *et al.* 2017) and higher order effects (Grilli *et al.* 2017). More specifically, the interpretations given for the two-species community still apply, that is a species can persist if $-\mathcal{F}_i < \frac{\mathcal{N}_i}{1-\mathcal{N}_i}$ and the multispecies case fulfils the five constraints outlined above (Appendix B). These interpretations are valid when (1) invasion analysis is possible and (2) correctly predicts coexistence, (Turelli 1978; Chesson 1994, 2000). In multispecies communities, but in some two-species communities as well, (1) and (2) will sometimes not be met (Barabás *et al.* 2018; Saavedra *et al.* 2017).

APPLICATIONS

Application to community models

The new definitions of $\mathcal{N}$ and $\mathcal{F}$ are applicable across various community types, driven by a variety of species interactions. To demonstrate this, we apply the definitions to five classic community types, and examine how the various growth rates and resulting c_i, c_j, $\mathcal{N}$ and $\mathcal{F}$ change between these types. Application to an empirical community, where species interactions may or may not be known a priori, is illustrated in the next section.

A first step in applying eqns 4 and 5 to a model is the quantification of the factors c_i and c_j. The *c* convert species *i* to *j* and vice-versa, and so logically $c_j \cdot c_i = 1$. For example, if one tree influences resource levels 10 times more than a forb ($c_{tree} = 10$), the forb influences resource levels 10 times less than the tree ($c_{forb} = 1/10$). After conversion, both species thus have the same total influence on the environment. In Fig. 2a, we provide an example of two species consuming common resources. We converted their consumption rates such that total consumption is the same for both species (Fig. 2b): the white and the grey area are equal. This example highlights two results. First, the *c*, by equating the total influence on limiting factors, is needed to correctly compute niche differences. That is, they remove any effect fitness differences may have on niche overlap. Second, after conversion (Fig. 2b), both species now also happen to have the same proportion of shared limiting factors ($1 - \mathcal{N}_i$ = light grey region $= 1 - \mathcal{N}_j$). We can therefore find *c* by solving the equations.

$$1 - \mathcal{N}_i = 1 - \mathcal{N}_j \tag{9}$$

$$c_i \cdot c_j = 1 \tag{10}$$

In Box 1, we illustrate this first step, and the calculation of $\mathcal{N}$ and $\mathcal{F}$, for a MacArthur consumer-resource model. We then convert this model into the well-known Lotka–Volterra model to express $\mathcal{N}$ and $\mathcal{F}$ using interaction coefficients. This exercise highlight the following results. First, while $\mathcal{N}$ and $\mathcal{F}$ are species specific, they can be identical between species in

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[1] Assuming that $\mathcal{N}_i < 1$

Box 1. $\mathcal{N}$ and $\mathcal{F}$ for the MacArthur and Lotka–Volterra model

Consider a community of two species whose dynamics follow MacArthur 1970

$$\frac{1}{N_i}\frac{dN_i}{dt} = \sum_{l=1}^{m} u_{il}R_l - m_i \tag{11}$$

$$\frac{1}{R_l}\frac{dR_l}{dt} = K_l - R_l - \sum_{i=1}^{2} u_{il}N_i \tag{12}$$

where u_{il} is the rate at which species i consumes resource l, R_l is the density of resource l, m_i is the loss rate and K_l is the resource's carrying capacity. We assume that the resource dynamics are faster than the dynamics of the consumers, such that R_l is always at equilibrium. In that case, the model simplifies to MacArthur 1970:

$$\frac{1}{N_i}\frac{dN_i}{dt} = \sum_{l=1}^{m} u_{il}K_l - m_i - \sum_{l=1}^{m} u_{il}u_{jl}N_j - \sum_{l=1}^{m} u_{il}^2 N_i \tag{13}$$

Solving eqns 9 and 10 yields (Appendix C).

$$c_j = \sqrt{\frac{\sum_{l=1}^{m} u_{jl}^2}{\sum_{l=1}^{m} u_{il}^2}} \tag{14}$$

Thus, c indeed captures the species' total influence on limiting factors. Replacing the c's into the growth rates, one obtains (Appendix D):

$$N_j^* = \frac{\sum_{l=1}^{m} u_{jl}K_l - m_j}{\sum_{l=1}^{m} u_{jl}^2} \tag{15}$$

$$f_i(0,0) = \sum_{l=1}^{m} u_{il}K_l - m_i \tag{16}$$

$$f_i\left(0, N_j^*\right) = \sum_{l=1}^{m} u_{il}K_l - m_i - \sum_{l=1}^{m} u_{il}u_{jl}\frac{\sum_{l=1}^{m} u_{jl}K_l - m_j}{\sum_{l=1}^{m} u_{jl}^2} \tag{17}$$

$$f_i\left(c_jN_j^*, 0\right) = \sum_{l=1}^{m} u_{il}K_l - m_i - \sqrt{\frac{\sum_{l=1}^{m} u_{il}^2}{\sum_{l=1}^{m} u_{jl}^2}}\left(\sum_{l=1}^{m} u_{jl}K_l - m_j\right) \tag{18}$$

Finally, replacing these into eqns 4 and 5, one obtains (Appendix D):

$$\mathcal{N}_i = 1 - \frac{\sum_{l=1}^{m} u_{il}u_{jl}}{\sqrt{\sum_{l=1}^{m} u_{il}^2 \sum_{l=1}^{m} u_{jl}^2}} \tag{19}$$

$$\mathcal{F}_i = 1 - \frac{\sum_{l=1}^{m} u_{jl}K_l - m_j}{\sum_{l=1}^{m} u_{il}K_l - m_i}\sqrt{\frac{\sum_{l=1}^{m} u_{il}^2}{\sum_{l=1}^{m} u_{jl}^2}} \tag{20}$$

We now note that eqn 13 is equivalent to the Lotka–Volterra model ($\frac{1}{N_i}\frac{dN_i}{dt} = \mu_i - \alpha_{ii}N_i - \alpha_{ij}N_j$), where $\mu_i = \sum_{l=1}^{m} u_{il}K_l - m_i$, $\alpha_{ii} = \sum_{l=1}^{m} u_{il}^2$ and $\alpha_{ij} = \sum_{l=1}^{m} u_{il}u_{jl}$ are the intrinsic growth rate, the intraspecific interaction strength and interspecific interaction strength respectively. Plugging these expressions in eqns 4 and 5 recovers equations for $\mathcal{N}$ and $\mathcal{F}$ that are equivalent to the earlier versions of $\mathcal{N}$ and $\mathcal{F}$ in the Lotka–Volterra model (Chesson 1990, 2000, 2013):

$$\mathcal{N}_i = 1 - \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}} \tag{21}$$

$$\mathcal{F}_i = 1 - \frac{\mu_j}{\mu_i}\sqrt{\frac{a_{ji}a_{ii}}{a_{jj}a_{ij}}} \tag{22}$$

species pairs competing for shared resources. Indeed, changing i for j in eqn 19 shows that $\mathcal{N}_i = \mathcal{N}_j$. However, they cease to be identical when including more than two species, as can be seen from Fig. 2c. Indeed, niche overlap, and therefore $\mathcal{N}$, is species specific in that case. Second, the new definitions of $\mathcal{N}$ and $\mathcal{F}$, when applied to the Lotka–Volterra model, collapse to equivalent definitions for $\mathcal{N}$ and $\mathcal{F}$ previously found for the same model (Chesson 1990). This shows that these new definitions, which apply to any model (for which invasion analysis is possible and useful) still agree with the definitions found for this particular model. Third, c_i carries a biological interpretation: in the MacArthur model, c_i indeed increases with the total influence on limiting factors (see eqn 14). This shows why the conversion factors c_i differs completely from the scaling factors used in modern coexistence theory: the latter are weights used to partition invasion growth rates (Barabás *et al.* 2018; Chesson 1994; Ellner *et al.* 2019; Appendix C).

This last feature is independent of the specific model formulation, that is, it extends beyond the McArthur resource model to any model in which two species interact through resource consumption, resource consumption stimulates growth and species consume more of a resource when its availability is higher. In Appendix D, we show a mathematical proof that in such a model, increasing the resource consumption of species i will increase c_i, that is, c is linked to the total resource consumption of a species. Finding the c when species have positive effects on each other (for example by generating resources or by limiting the efficacy of a predator) requires additional considerations, which are discussed in Appendices B and D.

Finally, we apply eqns 4 and 5 to examine how the various growth rates underlying $\mathcal{N}$ and $\mathcal{F}$, as well as $\mathcal{N}$ and $\mathcal{F}$ itself, change across community types (Fig. 3) modelled using Lotka–Volterra equations (Appendix D). Priority effects occur when interspecific interactions are stronger than intraspecific interactions, that is $(f_i\left(0, N_j^*\right) < f_i\left(c_jN_j^*\right)$, Fig. 3 c and d). Neutrality occurs when $\mathcal{N} = \mathcal{F} = 0$ (Adler *et al.* 2007). Competitive exclusion represents the well-known case where $\mathcal{N}$ are not large enough to compensate for $\mathcal{F}$: only the competitive dominant (species i) persists (Chesson 2013; Ke & Letten 2018).

For the case of 'mix of competition and facilitation' (Zarnetske *et al.* 2013; Adler *et al.* 2018) and mutualism, one or both species have an invasion growth rate that is higher than their intrinsic growth rate: these species profit from other species and thus grow better together than alone. Therefore,

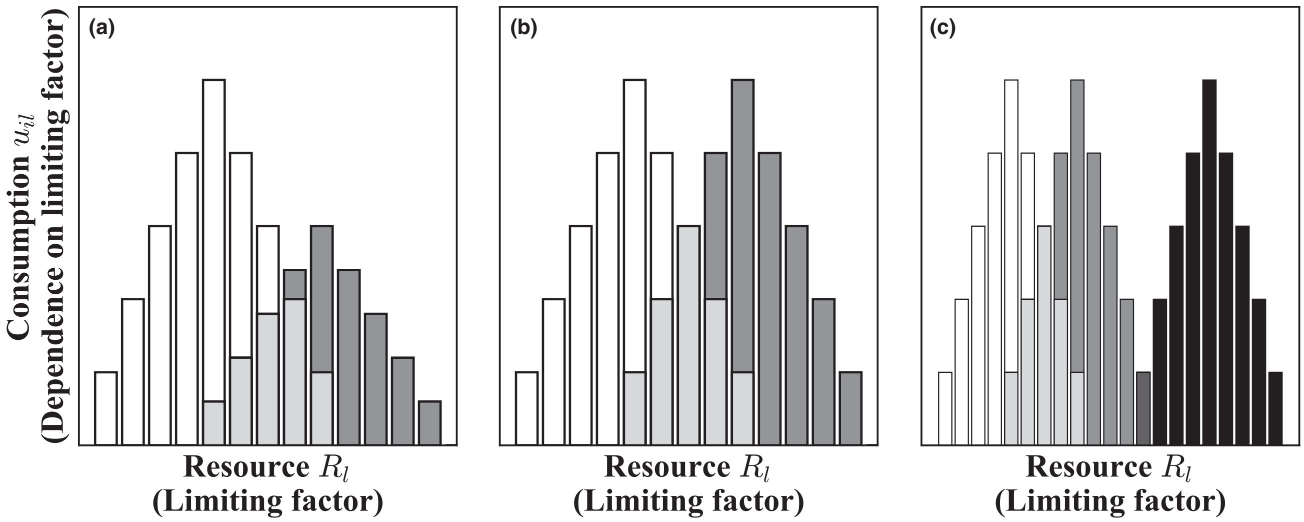

Figure 2 Species-specific influences on limiting factors (here, resources) for a two (a and b)- and a three (c)-species community. In the two-species community (a) the two species do not have the same total influence on the limiting factors, therefore the amount of shared resources is different ($1-\mathcal{N}_i = \frac{\text{light grey area}}{\text{white area}} \neq \frac{\text{light grey area}}{\text{grey area}} = 1-\mathcal{N}_j$). The conversion factors $c_i = \frac{\text{whitearea}}{\text{greyarea}}$ are chosen such that the two species have the same total effect on limiting factors (b). Then, the two species also share an equal proportion of their resources. This is, however, not the case in a multispecies community (c) (Adler *et al.* 2007), where the amount of shared resources is smaller for the black species than for the white species, even though all species consume the same total amount of resources. We therefore expect $\mathcal{N}_{\text{black}} \neq \mathcal{N}_{\text{white}}$.

these species have $\mathcal{N} > 1$. In these cases, $\mathcal{F}$ matter less for persistence (they only indicate the winner when $\mathcal{N} = 0$).

Application to experiments

The applicability of the new $\mathcal{N}$ and $\mathcal{F}$ definitions extends beyond models and can be used to analyse coexistence empirically. In these experiments, one needs to measure the various growth rates from eqns 4 and 5 to quantify $\mathcal{N}$ and $\mathcal{F}$ (Fig. 4). These experiments also allow estimating the factors c_i and c_j, giving insight in the species' total influence on limiting factors. Importantly, the definitions can be computed directly from the measured growth rates, without any assumption on the species'' ecology or the need to fit a model, in contrast to many other definitions. This is particularly useful since natural communities are typically governed by a multitude of species interactions, many of which will be unknown (Montoya *et al.* 2006; Carrara *et al.* 2015).

To illustrate the application to experimental data, we performed an experiment in which we measured growth of two picocyanobacteria species competing for light (Fig. 4). Detailed experimental methods can be found in the Appendix E. The two picocyanobacteria species contain different pigments (phycocyanobilin and phycoerythrobilin), which allow them to absorb different wavelengths of light (Fig. 4c; Six *et al.* 2007). Because light colour usages of these two species partly overlap, exactly as did resource usage in the MacArthur model (Fig. 2), we expected that $0<\mathcal{N}<1$ (i.e. species compete). Experiments and field data have shown that pigmentation differences among picocyanobacteria lead to a resource (light) partitioning that is sufficiently strong to allow coexistence (Stomp *et al.* 2004, 2007a,b). We therefore also expected that $-\mathcal{F} < \frac{\mathcal{N}}{1-\mathcal{N}}$ (i.e. coexistence).

Three growth curves per species suffice to quantify $\mathcal{N}$ and $\mathcal{F}$ for a two-species community (Fig. 4). First (Fig. 4a and b, triangles), we grew both species in a monoculture, starting from low density to obtain the intrinsic growth rate. Second (Fig. 4a and b, circles), we grew both species in a monoculture starting from a density higher than their equilibrium density to obtain the no-niche growth rate. The growth rate at which the density of the focal species reaches that of the converted equilibrium density of its competitor ($c_j N_j^*$) is the no-niche growth rate. In this particular case, the no-niche growth rates proved very small because $N_i^* \approx c_j N_j^*$ and $N_j^* \approx c_i N_i^*$. An example where this is not the case can be found in Fig. 5. Third (Fig. 4a and b, squares), we introduced each of both species into a monoculture at equilibrium of its competitor to obtain the invasion growth rates. More precisely, we introduced 5% of the invading species' equilibrium density (Narwani *et al.* 2013; Gallego *et al.* 2019). We estimated all these growth rates as $f_i(N_i(t), 0) \approx \log\left(\frac{N_i(t+\Delta t)}{N_i(t)}\right)/\Delta t$ with $\Delta t = 84\,\text{h}$. We then fitted a univariate spline to estimate these growth rates at the various densities. Finally, we were able to use the measured growth rates to solve the eqn 9 and thus obtain c_i and c_j, as well as $\mathcal{N}$ and $\mathcal{F}$. Importantly, the converted equilibrium density at which the no-niche growth rate is measured is part of the solution to these equations.

The results of the experiment confirmed our expectations: species compete for light ($0<\mathcal{N}<1$ for both species) and coexist (see triangle in Fig. 3). The estimated growth rates show that both species can grow independently of each other (positive intrinsic growth rate), and can invade each other's monoculture (positive invasion growth rate). Their no-niche growth rate is much smaller than their corresponding intrinsic growth rates, and slightly negative for species 1 but positive

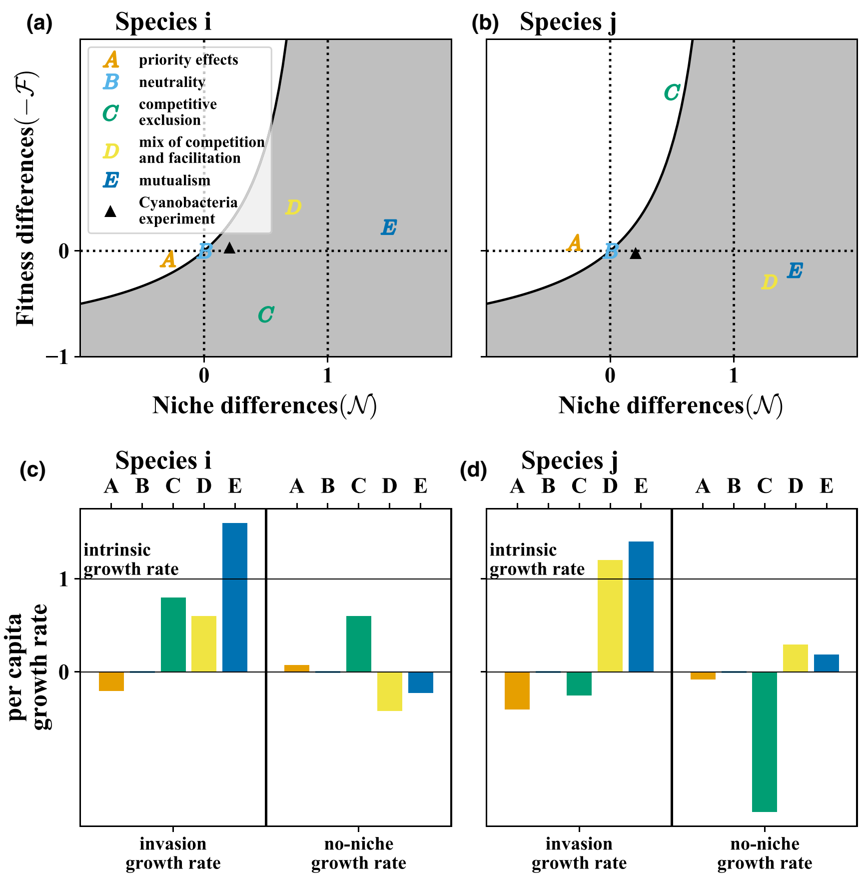

Figure 3 $\mathcal{N}$ and $\mathcal{F}$ applied to common two-species communities. Panels (a) and (b) show the distribution of $\mathcal{N}$ and $\mathcal{F}$ for species i and species j, respectively, where colour codes refer to different communities (see legend). (a–e) are communities simulated with Lotka–Volterra models, while 'experiment' refers to the performed experiment (Fig. 4). Only species in the grey area have a positive invasion growth rate, that is only those persist (Barabás *et al.* 2018; Chesson 2000). Panels (c) and (d) compares the invasion and the no-niche growth rate to the intrinsic growth rate (=1; vertical full line).

for species 2. This shows that removing all niche differentiation would lead to the exclusion of species 1, as is also seen from these species' fitness differences $\mathcal{F}$ (Fig. 3). Finally, we found the conversion factors c_i and c_j to match the relative total resource consumption (absorption) of the two species (Fig. 4d). This finding aligns with the theoretical result that the conversion factors link to the total influence on limiting factors (available resources) and confirms that these species compete for light. While this experimental procedure is applied to fast-growing communities, this design can be applied to communities with slow-growing species as well. Any method that allows estimating per capita growth is sufficient, but obviously these methods will vary with the considered community. For annual plants, for example, one may sow different quantities of seeds, ranging from low to above equilibrium density, in plots, and measure their growth.

DISCUSSION

In this article, we propose new definitions for $\mathcal{N}$ and $\mathcal{F}$ that are biologically intuitive by design. The approach is similar to Carroll *et al.* (2011) in that it allows computing $\mathcal{N}$ and $\mathcal{F}$ from simulations or experimental data, without the knowledge of the underlying mechanisms. When applied to the Lotka–Volterra model for competing species, the definitions collapse to equivalent mathematical expressions of $\mathcal{N}$ and $\mathcal{F}$ found before (Chesson 1990, 2013), while still being applicable to a large body of community models. This indicates that there is a potential for these new definitions to unify existing definitions (Barabás *et al.* 2018; Chesson 2000; Carroll *et al.* 2011; Godoy & Levine 2014), while enforcing the connection between theory and biological intuition (Adler *et al.* 2007, 2010; HilleRisLambers *et al.* 2012).

Specificities and limitations

$\mathcal{N}$ and $\mathcal{F}$, as defined in this paper, differ from other definitions of niche and fitness differences. Most notably, the proposed definitions are not based on specific mathematical models, apply to communities with positive species interactions and/or more than two species and allow inference of coexistence or exclusion. Thus, the new definitions notably extend modern coexistence theory based on invasion analyses. The structural approach of Saavedra *et al.* (2017) is the only definition for niche and fitness differences which can analyse communities that are outside the scope of this new definition,

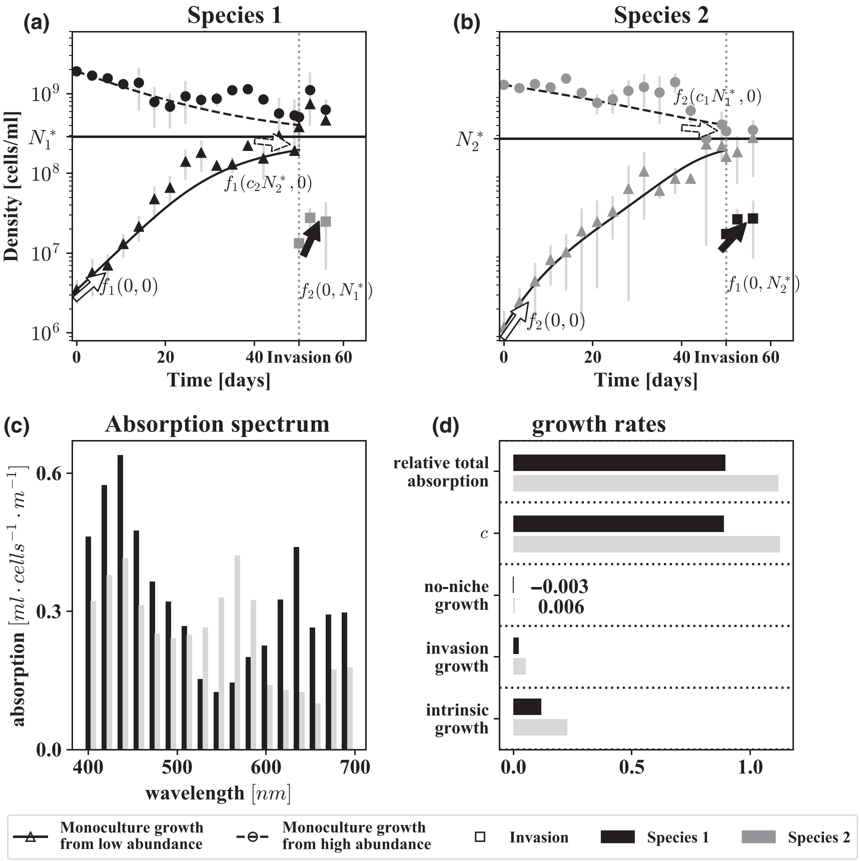

Figure 4 $\mathcal{N}$ and $\mathcal{F}$ applied to experimental data for two marine cyanobacteria species from the genus *Synechococcus*, sampled in the Baltic sea Stomp *et al.* 2004. (a and b) Population growth in the different experiments with different starting conditions. Fitted lines are obtained by interpolating growth rates. Importantly, to compute $\mathcal{N}$ and $\mathcal{F}$ one does not have to fit a community model through the measured densities. The arrows indicate the growth rates we measured to quantify $\mathcal{N}$ and $\mathcal{F}$. Error bars (grey) show one standard deviation (three replicates). (c) The two species have different absorption spectra and therefore partition light usage. A spectrum of the incoming light intensity can be found in Appendix E. (d) The experiment confirms that the species compete and coexist, as the invasion growth rate is positive, but smaller than the intrinsic growth rate. The conversion factor c is very similar to the relative total absorption of the two species, confirming its interpretation as a measure of total influence on the limiting factors (see eqn 14). An automated code to compute $\mathcal{N}$ and $\mathcal{F}$ from such experimental data can be found on https://doi.org/10.6084/m9.figshare.12000840.v1.

as it does not depend on invasion analysis. They define $\mathcal{N}$ and $\mathcal{F}$ for a community in which the equilibrium point of the community can be described as $r = \alpha N^*$, where α is a n by n matrix containing the species interactions and r is a vector containing the intrinsic growth rates (or equivalent), which may be subject to additional constraints (Song *et al.* 2018). Finally, there are still communities that are beyond the reach of all definitions for $\mathcal{N}$ and $\mathcal{F}$, including the newly proposed definitions: multispecies communities with nonlinear interspecific species interactions (therefore excluding the approach of Saavedra *et al.* (2017), but see Cenci & Saavedra 2018), and not allowing invasion analysis (therefore excluding the approaches of Carmel *et al.* (2017); Carroll *et al.* (2011); Chesson (2003) and the definitions proposed here).

The reliance on invasion analysis is a first limitation of the proposed definitions, as it is for many other definitions (Chesson 2003; Carroll *et al.* 2011; Zhao *et al.* 2016; Carmel *et al.* 2017). This reliance means that one should be able to compute the invasion growth rate for each species and that the invasion growth rates correctly predict coexistence. This can limit the applicability of the definitions in two ways. First, there will be communities in which invasion analysis does not correctly predict coexistence (Barabás *et al.* 2018). An example is the annual plant model combined with positive frequency dependency proposed by Schreiber *et al.* (2019). Second, invasion analysis requires that all species within each S-1 subcommunity (the community without the invading species) stably coexist. A well-known counter example is the rock–paper–scissor community, in which the whole community can coexist, while each two-species subcommunity is not stable (Grilli *et al.* 2017). While these two assumptions will be met for most two-species communities, we expect they will be increasingly violated as communities contain more species (Saavedra *et al.* 2017).

A second limitation of the new definitions is the difficulty of interpretation that arises in communities with Allee effects. The proof that the c_i have a unique solution demands Allee effects to be absent (see Appendix B). Consequently, Allee effects imply that species may have multiple $\mathcal{N}$ and $\mathcal{F}$. This highlights the meaning of Allee effects: species change their

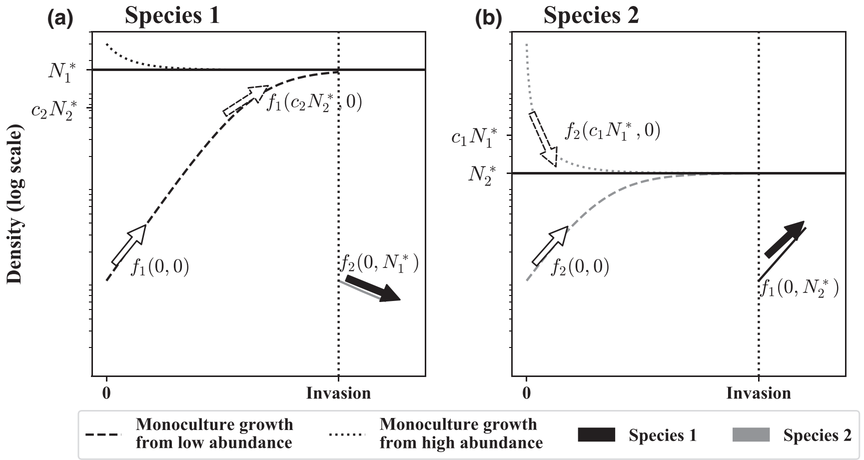

Figure 5 $\mathcal{N}$ and $\mathcal{F}$ applied to simulated experimental data using case c from Figure 3, where $c_1N_1^*$ ($c_2N_2^*$) and N_2^* (N_1^*) differ substantially, unlike in Figure 4. For the competitive inferior (species 2), we have $c_1N_1^* > N_2^*$, while for the other species (species 1) we have, $c_2N_2^* < N_1^*$. For species 1 the second experiment (dotted black line) proved not necessary to compute $\mathcal{N}$ and $\mathcal{F}$, as the no-niche growth rate can be estimated from experiment 1 (dashed arrow, dashed black line). However, in general one will not know in advance for which species experiment 2 is unnecessary.

dependence on limiting factors with their density. While the new definitions do allow computing these multiple $\mathcal{N}$ and $\mathcal{F}$, it is at present not clear how to interpret them.

The need for new definitions

With already 10 definitions at hand, one may ask why we need new definitions for niche and fitness differences. We identify at least two reasons. A first reason deals with the complexity of many community models. Many approaches to compute niche and fitness differences first fit a community model to empirical data and then perform maths to link the model to $\mathcal{N}$ and $\mathcal{F}$ (Chesson 1990; Godoy & Levine 2014; Saavedra *et al.* 2017; Bimler *et al.* 2018). One challenge is that these maths are often non-trivial (e.g. Carmel *et al.* (2017); Godoy & Levine (2014); Saavedra *et al.* (2017)) and one needs to resort into simplifying the community model (Godoy & Levine 2014; Letten *et al.* 2017). This may lead to the omission of mechanisms contributing to $\mathcal{N}$ (Chu & Adler 2015). For example, niche partitioning could arise at different life stages of a species (Moll & Brown 2008), or through its interactions with resources (Chesson 1990), predators (Chesson & Kuang 2008) or mutualists (Johnson & Bronstein 2019) and will be affected by environmental change (Rey *et al.* 2017; Wainwright *et al.* 2019). An important advantage of the new definitions is that they do not require analytical solutions of a community model or even a community model at all; one can simply simulate or perform the experiments described in the section 'Application to experiments' and measure the resulting growth rates to compute $\mathcal{N}$ and $\mathcal{F}$. Thus, the model or experimental community can be used in its full complexity, capturing all mechanisms potentially contributing to $\mathcal{N}$ and $\mathcal{F}$.

A second reason is that the analysis of communities with non-competitive interactions (e.g. mutualistic and facilitative; Fig. 1) and multiple species (eqn 7) is urgently needed. Indeed, such communities have often been analysed in a suboptimal way. For example Narwani *et al.* (2017) tested whether closely related freshwater green algae are more likely to coexist due to higher niche differentiation. However, $\mathcal{N}$ could not be computed when species interactions were positive. Similarly, in a meta-analysis on terrestrial plants, Adler *et al.* (2018) were not able to compute $\mathcal{N}$ for one third of the data, as they contained positive interactions. Chu & Adler (2015) measured $\mathcal{N}$ and $\mathcal{F}$ in an age-structured model for perennial plants fitted to long-term demographic data, Petry *et al.* (2018) measured the effects of ant consumption on $\mathcal{N}$ and $\mathcal{F}$ and Veresoglou *et al.* (2018) reanalysed data from the 'BIODEPTH' grassland biodiversity experiment. While these studies do report computed $\mathcal{N}$ and $\mathcal{F}$ for multispecies communities, the interpretation of these variables is difficult, as they do not predict coexistence in multispecies communities.

New insights and outstanding questions

Historically, $\mathcal{N}$ measured the proportion of resources not shared by two species (Hurlbert 1978). Being a proportion, $\mathcal{N}$ was bound between 0 and 1 (Godoy & Levine 2014). Linking a mechanistic (resource uptake) model to the Lotka–Volterra model (MacArthur 1970; Chesson 1990) was a key step in exploring $\mathcal{N}$ beyond the traditional range $[0, 1]$. Recent research interpreted negative $\mathcal{N}$ as a sign that interspecific interactions are stronger than intraspecific interactions, leading to priority effects (Ke & Letten 2018). The interpretation that $\mathcal{N}$ greater than 1 imply positive interspecific interactions is a logical next step. Our results show that this interpretation is correct when both species have symmetric positive effects on each other, but also that species benefiting from other species (e.g. 'mix of competition and facilitation' in Fig. 3) would have $\mathcal{N} > 1$.

The results suggest that $\mathcal{N}$ and $\mathcal{F}$ are species-specific properties. While this idea has already been introduced by Adler *et al.* (2007), virtually all other definitions consider $\mathcal{N}$ a community property. This likely stems from the fact that most definitions focus on two-species communities with competitive interactions, in which case niche differences are the proportion of shared resources, which is the same for both species (Fig. 2b, light grey area). Therefore, in this particular case, the two species have the same $\mathcal{N}$, leading to the impression that $\mathcal{N}$ is a community property.

The results spur three outstanding questions on species coexistence. A first question deals with the variable c, that we found increases with the total influence on limiting factors, both for a class of resource competition models and empirically. However, our mechanistic understanding of these factors is absent for models beyond the ones considered here, notably in systems not driven by resource competition. Most notably, we do not know how c relates to the presence of limiting factors with negative effects on per capita growth. A second outstanding question deals with the location of species from complex communities on the $\mathcal{N}$ and $\mathcal{F}$ planes from Fig. 3. While these positions may be trivial in some two-species communities, they will not be in large complex networks with a high number of indirect effects, possibly leading to surprising conclusions regarding the contribution of stabilising and equalising forces to persistence. A third question deals with the extended applicability the new definitions offer to modern coexistence theory. This applicability would allow asking how $\mathcal{N}$ or $\mathcal{F}$ compare across community types, mechanisms and environments. Thus, the new definitions enable cross-community comparisons in a way that at present is not possible. One could, for example, examine how species from different community types position in Fig. 3, to ask if community types that are thought to harbour a more diverse set of mechanisms fostering coexistence (e.g. annual plants) distinguish from community types that appear to have little possibilities for niche differentiation (e.g. phytoplankton (Hutchinson 1959)).

Within a community type (e.g. phytoplankton), one could compare the stabilising effect of various mechanisms. For example, we found $\mathcal{N}$ and $\mathcal{F}$ to indicate coexistence in a classic example of a community driven by partitioning of the light spectrum through phenotypic differences (i.e. pigmentation, see Fig. 4; Stomp *et al.* 2004). How does the stabilising strength of these phenotypic differences (driving $\mathcal{N}$) compare to the strength of other relevant mechanisms (e.g. competition for mineral nutrients, allelopathy)? One could also examine how environmental changes alter the sign of species interactions (Baert *et al.* 2016; Olsen *et al.* 2016; Song *et al.* 2020) impact the persistence, since the proposed definitions accommodate various interaction types.

In conclusion, our results offer a new perspective on two concepts that underpin biodiversity science, and foster their intuitive biological interpretation (Fig. 1). The developed theory is applicable to a variety of ecological communities, regardless of community complexity, and without the need of mathematical skills (Ellner *et al.* 2019), for any system in which invasion analysis is possible and correctly determines coexistence. The fact that various communities can be analysed with one approach is a major step forward. Taken together, the novel definitions of $\mathcal{N}$ and $\mathcal{F}$ promote conceptual unification and facilitate empirical research in community ecology and biodiversity science.

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AUTHORSHIP

J.W.S. and F.D.L. developed the ideas and wrote the manuscript. J.W.S. developed and implemented the mathematical theory.

DATA AVAILABILITY STATEMENT

The code to compute $\mathcal{N}$ and $\mathcal{F}$ as well as to produce all figures will be archived on Zenodo. Data obtained from the experiment will be included in the repository (https://doi.org/10.6084/m9.figshare.12000840.v1).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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