A unified definition of niche and fitness differences

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Explaining nature's biodiversity is a key challenge for science[1]. To persist against a background of interacting species with potentially higher fitness, populations must be able to grow faster when rare, a feature called negative frequency dependence[2–4]. Coexistence theory quantifies this dependence as niche differences ($\mathcal{N}$), but the available definitions differ greatly in how $\mathcal{N}$ should vary with the type of species interactions, and often apply to specific community types only. Here, we present a new definition of $\mathcal{N}$ that is consistent with biological intuition and can be applied to communities driven by both negative and positive species interactions, filling a main gap in the literature[5,6]. We also derive a definition for the corresponding fitness differences ($\mathcal{F}$) among species, and illustrate how $\mathcal{N}$ and $\mathcal{F}$ jointly determine coexistence for various community types. We demonstrate that our definitions can be operationalised with theoretical models and experimental data. Our definition qualifies as the first method to quantify $\mathcal{N}$ and $\mathcal{F}$ in a standardised way across theoretical and empirical communities, facilitating comparison and fostering synthesis in community ecology.

Species can partition resources[3,7], predators[8–10], or microhabitats[11], or can lack mates when rare[12]. What all these mechanisms have in common is that they generate frequency dependence: population growth depends on the species relative density, i.e. it's frequency. Niche difference is the collective name for all such mechanisms contributing to frequency dependence[2,13]. In 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[3,4,14,15]. Without niche differences, one of the species will eventually exclude all others; the rate of exclusion measures the competitive advantage the winning species would have in the absence of frequency dependence. This competitive advantage is often called the average fitness difference[4,14,16], or just fitness difference for short.

A key question is if niche differences in natural systems are strong enough to overcome fitness differences and thus save species from extinction[5,17–22].

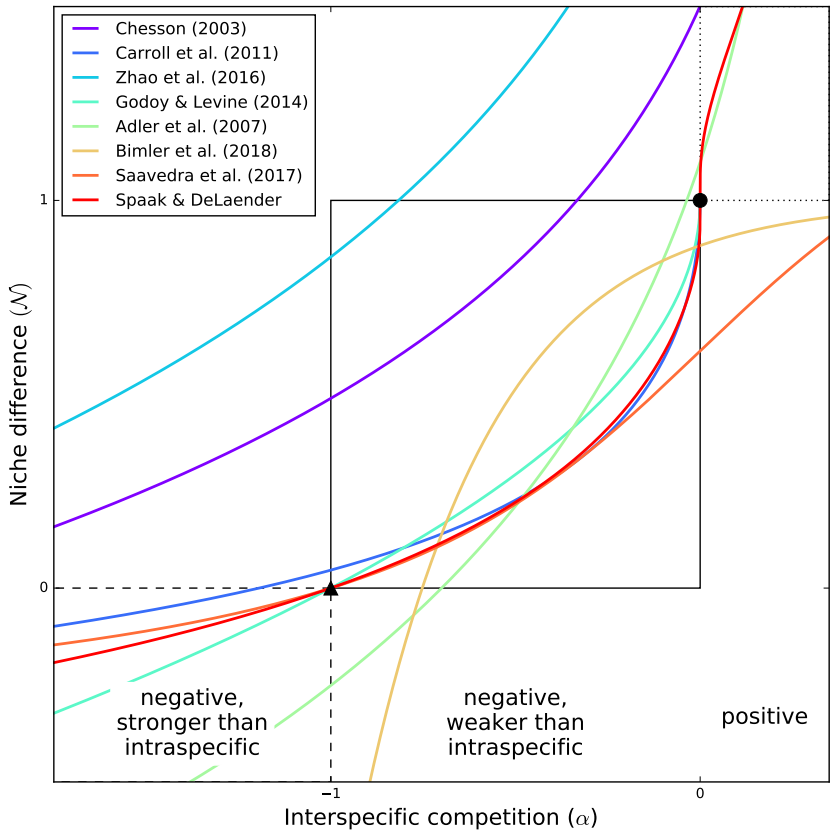


Figure 1: **Niche differences ($\mathcal{N}$) between two plant species respond to the interspecific competition strength α. However, different definitions of $\mathcal{N}$ and $\mathcal{F}$ applied to the community type (annual plant model) lead to different responses of $\mathcal{N}$ to α. The black dot indicates where species do not interact ($\alpha = 0$), and so species have completely different niches (i.e. $\mathcal{N}$ should be 1). Consequently, communities in which interspecific interactions are positive ($\alpha > 0$) should have $\mathcal{N}$ larger than 1 (dotted rectangle). The black triangle indicates where inter- and intraspecific interactions are equal (i.e. the species occupy the same niche and $\mathcal{N}$ should be 0). . Again, communities with stronger interspecific interactions must have $\mathcal{N} < 0$ (dashed 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 (Spaak & DeLaender, in red) is the only that complies with these 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 the appendix 1.**

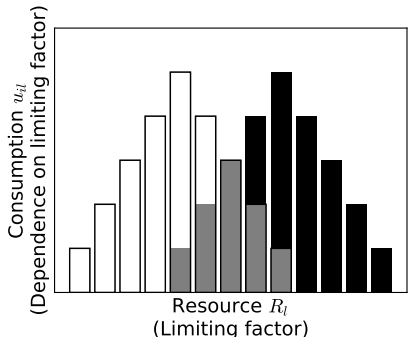
Scientists have addressed this question with various experimental and theoretical methods, while there is no consensus what niche and fitness differences are, and how they can be quantified across the variety of community types observed in nature. Indeed, people have been grappling with the proper operationalisation of these concepts for almost a century[4,14,23–28] and existing definitions often apply to specific communities only. In addition, all but two of the available definitions require an explicit mathematical model of the underlying species interactions (for the exceptions, see[27,29]), hampering empirical study of communities driven by processes yet to be uncovered.

There are currently nine different definitions for niche and fitness differences ($\mathcal{N}$ and $\mathcal{F}$, Appendix 1). Five of these apply to one specific model only[3,8,26,28,30]. The other four can be applied to a larger class of models[14,27,29,31]. Seven of them can be applied to the annual plant model, a workhorse of theoretical ecology[3,7,15,17,32–34]. Doing so shows that different definitions imply different $\mathcal{N}$ despite the same underlying community type (Fig. 1). In addition, these values do not readily translate to $\mathcal{N}$ values that align with biological intuition, which renders interpretation challenging.

Biological intuition constrains the values that $\mathcal{N}$ should take. When intra- and interspecific interactions are of equal size, such that individuals of the species are interchangeable, $\mathcal{N}$ should equal 0 as both species share the same niche (black triangle in Fig. 1). When interspecific interactions are absent, each species operates in its own niche and so $\mathcal{N}$ should be one hundred percent, or 1 (i.e. niches are 100% different; black dot in Fig. 1). Logically, intermediate interspecific interaction strengths should result in $\mathcal{N}$ between 0 and 1 (solid rectangle in Fig. 1). At greater inter- than intraspecific competition, species interact more strongly with each other than they would if they were in the same niche. Therefore, $\mathcal{N}$ should be negative (dashed rectangle in Fig. 1). Finally, when interspecific interactions are positive, e.g. because of facilitation, $\mathcal{N}$ should be greater than 1 (dotted rectangle in Fig. 1).

Box 1: Application to models

Applying the definitions of eqs. 4 and 5 to a community model demands quantifying the factors c_j. These factors convert species i to j and vice-versa (such that $c_j \cdot c_i = 1$) and make sure that both species have the same total dependence on limiting factors, which is needed since $\mathcal{N}$ should measure relative, not absolute, differences of the dependence on limiting factors. Fig. 2 shows that when both species have the same total dependence on limiting factors (i.e. the white and the black area are equal), the proportion of limiting factors shared with the other species ($1 - \mathcal{N}$, grey region) is equal for both species. We can therefore find c_j by solving the equation $1 - \mathcal{N}_i = 1 - \mathcal{N}_j$.



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

$$\frac{1}{R_l}\frac{dR_l}{dt} = r_l\left(1 - \frac{R_l}{K_l}\right) - \sum_{i=1}^{n} u_{il} N_i$$

Figure 2: **Dependence of two species (white and black) on limiting factors. In the MacArthur resource model the limiting factors are the resources R_l and the dependence is the consumption u_{il}.**

As an example, we took the MacArthur resource model (above equations), 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, r_l is the maximal rate at which resource l is regenerated and K_l is the resource's carrying capacity. For the species i of the MacArthur resource model one obtains (Appendix 3):

$$\mathcal{N}_i = 1 - \frac{\langle u_i, u_j \rangle}{\|u_i\| \cdot \|u_j\|}; \qquad \mathcal{F}_i = 1 - \frac{\mu_j}{\mu_i}\frac{\|u_i\|}{\|u_j\|}; \qquad c_i = \frac{\|u_j\|}{\|u_i\|}$$

Where $\langle u_i, u_j \rangle = \sum_{l=1}^{m} u_{il} u_{jl} \frac{K_l}{r_l}$ and $\|u_i\| = \sqrt{\langle u_i, u_i \rangle}$ can be thought of the grey, and white respectively black area in Fig. 2. $\mu_i = \sum_{l=1}^{m} u_{il} K_l - m_i$ is the monoculture growth rate of the species. Hence we see that c_i indeed scales the total dependence on limiting factors. This approach can be adapted to apply to more complex situations as well, e.g. when species have positive effects on each other by generating resources or limit the efficacy of a predator. In that case, species will have a negative total dependence on limiting factors. In that case the c_j cannot be used to equate a negative (e.g. of the resource-producing species) with a positive total dependence (of the resource-consuming species), as the c_j are strictly positive. We show in appendix 2 that solving $|1 - \mathcal{N}_i| = |1 - \mathcal{N}_j|$ yields a solution for c_j. A code to compute the c_j, $\mathcal{N}$ and $\mathcal{F}$ for any model can be found on https://github.com/juergspaak/NFD_definitions.

What would a definition of $\mathcal{N}$ need to look like to align with biological intuition? The per capita growth of a species i reads

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

where N_i, N_j are the densities of species i and a species j ($i \neq j$) with which i interacts. We assume that the per capita growth rates (f_i) in monoculture are maximal when species have very low density: $f_i(0,0) > f_i(N_i,0)$.

The constraint that $\mathcal{N}$ should be 1 in the absence of species interactions mathematically translates to

$$\mathcal{N} = 1 \Rightarrow f_i(N_i, N_j) = f_i(N_i, 0) \tag{2}$$

The constraint that $\mathcal{N}$ should be 0 when inter- and intraspecific interactions are equal yields

$$\mathcal{N} = 0 \Rightarrow f_i(N_i, N_j) = f_i(N_i + c_j N_j, 0) \tag{3}$$

Here, 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. Equations 1-3 hold for all densities N_i, N_j, but measuring the strength of frequency dependence for a focal species i is typically done by inspecting how f_i behaves when i is at low frequency, i.e. when $N_i \approx 0$ and j is at its monoculture equilibrium N_j^*. In this scenario eqs. 2 and 3 become $\mathcal{N} = 1 \Rightarrow f_i(0, N_j^*) = f_i(0,0)$ and $\mathcal{N} = 0 \Rightarrow f_i(0, N_j^*) = f_i(c_j N_j^*, 0)$. Here $f_i(0, N_j^*)$ is the invasion growth rate, $f_i(0,0)$ is the monoculture growth rate and $f_i(c_j N_j^*, 0)$ we term the no-niche growth rate.

Interpolation then results in

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

Here we assume $c_j = 1$ for notational simplicity, but illustrate how to quantify c_j in box 1. The new definition of $\mathcal{N}$ has a clear biological interpretation. $\mathcal{N}$ compares the interspecific competition $f_i(0, N_j^*)$ with intraspecific competition $f_i(N_j^*, 0)$[4,30]. The total density is the same (N_j^*) in both terms but the frequency of the species i differs, being 0% in $f_i(0, N_j^*)$ and 100% in $f_i(N_j^*, 0)$. $\mathcal{N}$ therefore measures frequency dependence[3,7]. In addition, eq. 4 aligns with the biological constraints outlined above and in Fig. 1, as it meaningfully maps three possible cases of species interactions into three ranges of $\mathcal{N}$. To illustrate this, we applied this definition to the same annual plant model discussed

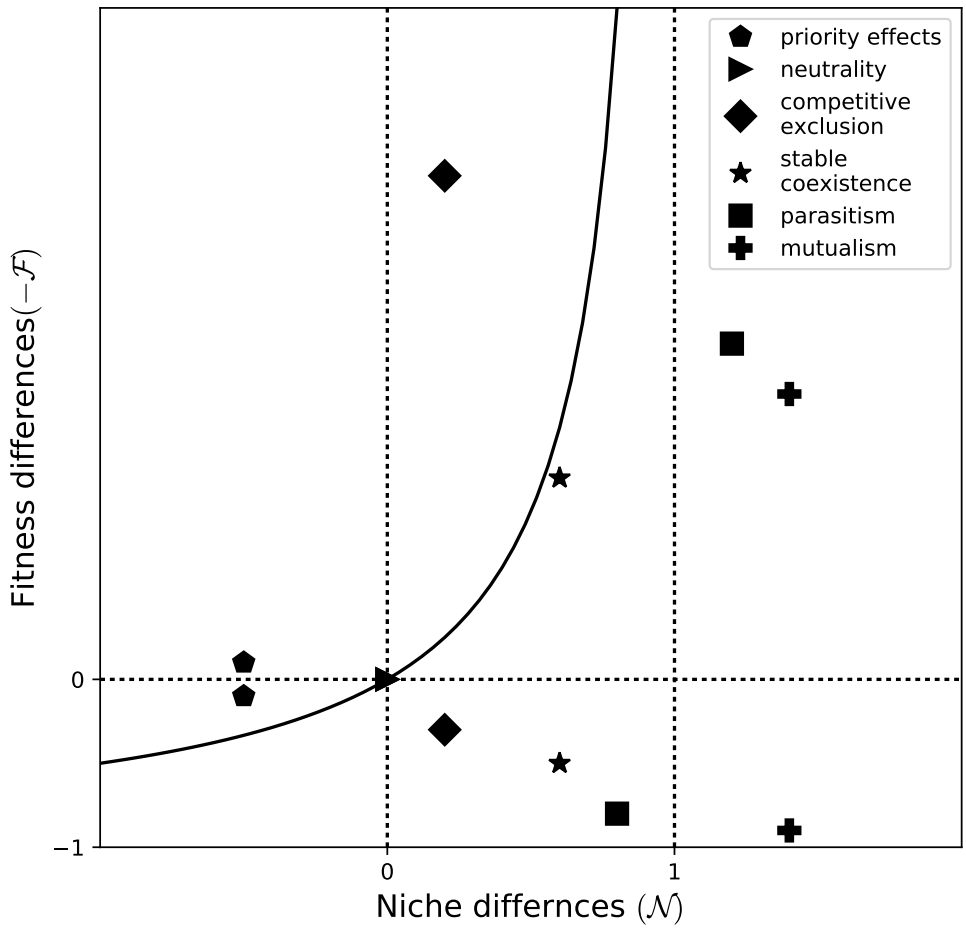


Figure 3: **Examples of $\mathcal{N}$ and $\mathcal{F}$ for the most common community types, applied to two-species communities. Species in the grey area have a positive invasion growth rate ($f_i(0, N_j^*)$), i.e. they persist. If both species have positive invasion growth rates the species are assumed to coexist[4,16]. The $\mathcal{N}$ values of the species satisfy the equation $|1 - \mathcal{N}_i| = |1 - \mathcal{N}_j|$ (Box 1). However, the $\mathcal{F}$ values of the two species are independent. Community types are: competitive exclusion (one species excludes the other, regardless of the initial condition), priority effects (competitive exclusion where the winner depends on the initial condition), neutrality (competitive exclusion, where the winner of competition depends on chance), stable coexistence, parasitism (one species is negatively affected by, and benefits, the other), mutualism (both species benefit each other).**

above (https://github.com/juergspaak/NFD_definitions). When species interact negatively and do so more within than between species, $\mathcal{N}$ is bounded in $[0,1]$ (solid rectangle Fig. 1). However, when interspecific competition is stronger than intraspecific competition ($f_i(0,N_j^*) < f_i(N_j^*,0)$) $\mathcal{N}$ will be negative (dashed rectangle, Fig. 1). In such a case $\mathcal{N}$ can never support coexistence, as species have a positive frequency dependence: species grow faster when abundant[35,36]. On the other hand, when interspecific effects are positive ($f_i(0,0) < f_i(0,N_j^*)$) $\mathcal{N}$ is larger than 1 (dotted rectangle, Fig. 1).

Our novel definition of $\mathcal{N}$ has important consequences for how the fitness difference $\mathcal{F}$ is mathematically defined. Verbally, $\mathcal{F}$ is the difference in intrinsic growth rate between species when both species have the same niche, i.e. $\mathcal{N} = 0$[15,16]. Therefore

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

$\mathcal{F}_i$ ranges from $-\infty$ to 1 and measures the difference in normalized species growth rate when all frequency dependence has been removed[3,15] i.e., as if we had put species j into species i's niche. When $\mathcal{F}_i$ is 0 both species are equally competitive. Note that the second term of eq. 5 is 0, which shows that $\mathcal{F}_i$ is identical to the normalized species growth rate of species i in absence of frequency dependence.

The developed equations for $\mathcal{N}$ and $\mathcal{F}$ can be generalised to multispecies communities (Appendix 2):

$$\mathcal{N}_i = \frac{f_i(0,\boldsymbol{N}^{-i,*}) - f_i(\sum_{j\neq i} c_j^i N_j^{-i,*},\mathbf{0})}{f_i(0,\mathbf{0}) - f_i(\sum_{j\neq i} c_j^i N_j^{-i,*},\mathbf{0})} \tag{6}$$

$$\mathcal{F}_i = \frac{f_i(\sum_{j\neq i} c_j^i N_j^{-i,*},\mathbf{0})}{f_i(0,\mathbf{0})} \tag{7}$$

Here, c_j^i converts densities of species j into i, $\boldsymbol{N}^{-i,*}$ is the vector of equilibrium densities in the absence of species i, and $\mathbf{0}$ denotes the absence of all species other than i. These definitions represent the net effect of species interactions on $\mathcal{N}$ and $\mathcal{F}$, i.e. direct, indirect[37] and higher order effects[38]. Importantly, the interpretations given for the two-species community still apply. Species persist when their invasion growth rates $f_i(0,\boldsymbol{N}^{-i,*})$ are positive[4,39,40]. Interestingly, normalising the invasion growth rate by the monoculture growth rate $f_i(0,0)$ yields (Appendix 2)

$$\frac{f_i(0,\boldsymbol{N}^{-i,*})}{f_i(0,0)} = \mathcal{N}_i + \mathcal{F}_i - \mathcal{N}_i \cdot \mathcal{F}_i \tag{8}$$

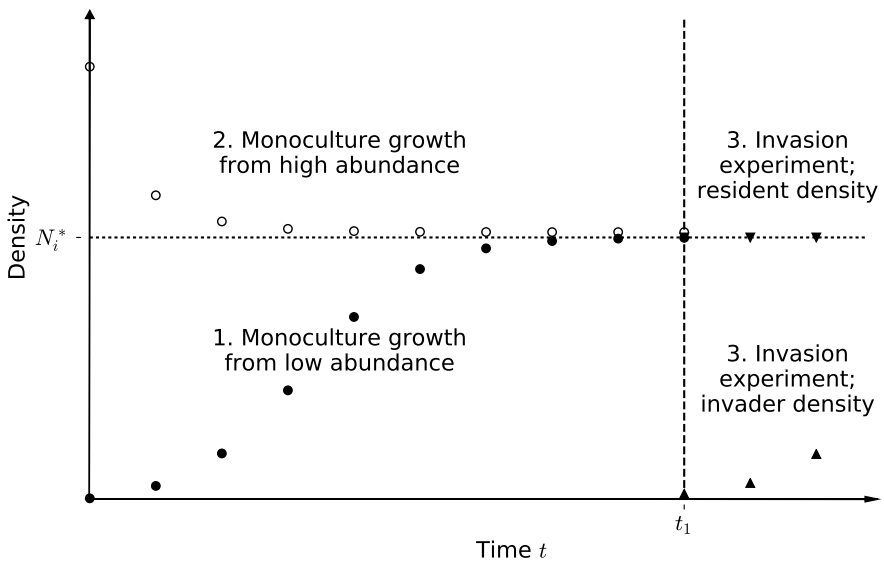


Figure 4: **Three growth curves per species suffice to quantify $\mathcal{N}$ and $\mathcal{F}$ for a two-species community: (1, black circles) grow both species i and j in a monoculture starting from low density to obtain $f_i(0,0)$ and $f_i(c_j N_j^*,0)$; (2, empty circles) grow species i and j in a monoculture starting from a density higher than equilibrium density to obtain $f_i(c_j N_j^*,0)$; (3, triangles) measure the invasion growth rates of both species to obtain $f_i(0,N_j^*)$. An automated code to compute $\mathcal{N}$ and $\mathcal{F}$ from such experimental data can be found on https://github.com/juergspaak/NFD_definitions.**

Thus, i can persist within the community when[1]:

$$-\mathcal{F}_i < \frac{\mathcal{N}_i}{1-\mathcal{N}_i} \tag{9}$$

Apart from formalising $\mathcal{N}$ and $\mathcal{F}$ in a way that is independent of the study system, our definitions can be applied to models (Box 1) and to experimental studies. Straightforward experiments with varying starting densities suffice to quantify $\mathcal{N}$ and $\mathcal{F}$ (Fig. 4). These experiments allow measuring the factor c_i, giving insight in the total dependence on limiting factors of each species. Importantly, our definitions can be applied directly to the measurements of the

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

experiment and do not require any assumption on population growth as do many other definitions for $\mathcal{N}$ and $\mathcal{F}$. This is particularly useful since natural communities are typically governed by a multitude of species interactions, many of which will be unknown[41]. However, this also highlights a key challenge when empirically assessing $\mathcal{N}$ and $\mathcal{F}$: In multispecies communities, the experimental work will be tremendous ($2n$ monoculture, $n(n-1)$ invasion and n multispecies experiments), making the quantification of $\mathcal{N}$ and $\mathcal{F}$ challenging if not prohibitive in species-rich communities.

A first feature of our definition of $\mathcal{N}$ is that it fosters an intuitive biological interpretation of how similarities and differences among species map to the persistence of species and communities (Fig. 1). A second feature is that our definitions can be operationalised in a variety of ecological communities, regardless of community complexity (the number of species, eq. 6) or the kind of species interactions (priority effects, neutrality, competitive exclusion, coexistence, parasitism, and mutualism, Fig. 3). Importantly, theory to analyse communities with non-competitive, such as mutualistic and trophic, interactions for $\mathcal{N}$ and $\mathcal{F}$ has been lagging behind empirical work. Our theory provides the tools to analyse data of such communities, which were often left treated improperly in former coexistence studies in spite of a theoretical framework[5,6]. Taken together, the novel definitions of $\mathcal{N}$ and $\mathcal{F}$ we present here promote conceptual unification and facilitate empirical research in community ecology and biodiversity science.

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References

[1] G. E. Hutchinson. Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22(0):415–427, 1957.

[2] J. HilleRisLambers, P.B. Adler, W.S. Harpole, J.M. Levine, and M.M. Mayfield. Rethinking Community Assembly through the Lens of Coexistence Theory. *Annual Review of Ecology, Evolution, and Systematics*, 43(1):227–248, 2012.

[3] Peter B. Adler, Janneke HilleRislambers, and Jonathan M. Levine. A niche for neutrality. *Ecology Letters*, 10(2):95–104, 2007.

[4] Peter Chesson. Mechanisms of maintenance of speciesdiversity. *Annual Review of Ecology, Evolution, and Systematics*, 31, 2000.

[5] Peter B. Adler, Danielle Smull, Karen H. Beard, Ryan T. Choi, Tucker Furniss, Andrew Kulmatiski, Joan M. Meiners, Andrew T. Tredennick, and Kari E. Veblen. Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters*, 21(9):1319–1329, 2018.

[6] Chengjin Chu and Peter B Adler. Large niche differences emerge at the recruitment stage to stabilize grassland coexistence.pdf. *Ecological Monographs*, 85(3):373–392, 2015.

[7] Jonathan M. Levine and Janneke HilleRisLambers. The importance of niches for the maintenance of species diversity. *Nature*, 461(7261):254–257, 2009.

[8] Peter Chesson and Jessica J. Kuang. The interaction between predation and competition. *Nature*, 456(7219):235–238, 2008.

[9] Eric Allan, Jasper Van Ruijven, and Michael J. Crawley. Foliar fungal pathogens and grassland biodiversityAllan, E., Van Ruijven, J., & Crawley, M. J. (2010). Foliar fungal pathogens and grassland biodiversity. Ecology, 91(9), 25722582. *Ecology*, 91(9):2572–2582, 2010.

[10] Walter P. Carson and Richard B. Root. Herbivory and plant species coexistence: Community regulation by an outbreaking phytophagous insect. *Ecological Monographs*, 70(1):73–99, 2000.

[11] Jonathan Silvertown. Plant coexistence and the niche. *Trends in Ecology and Evolution*, 19(11):605–611, 2004.

[12] Franck Courchamp, Tim Clutton-Brock, and Bryan Grenfell. Inserve density dependence dans the Allee effect. *Tree*, 14(1984):405–410, 1999.

[13] Andrew D. Letten, Po Ju Ke, and Tadashi Fukami. Linking modern coexistence theory and contemporary niche theory. *Ecological Monographs*, 87(2):161–177, 2017.

[14] Peter Chesson. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. *Theoretical Population Biology*, 64(3):345–357, 2003.

[15] Peter B. Adler, Stephen P. Ellner, and Jonathan M. Levine. Coexistence of perennial plants: An embarrassment of niches. *Ecology Letters*, 13(8):1019–1029, 2010.

[16] György Barabás, Rafael D'Andrea, and Simon Maccracken Stump. Chesson's coexistence theory. *Ecological Monographs*, 2018.

[17] Amy L. Angert, Travis E. Huxman, Peter Chesson, and D. Lawrence Venable. Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences*, 106(28):11641–11645, 2009.

[18] Jacob Usinowicz, Chia Hao Chang-Yang, Yu Yun Chen, James S. Clark, Christine Fletcher, Nancy C. Garwood, Zhanqing Hao, Jill Johnstone, Yiching Lin, Margaret R. Metz, Takashi Masaki, Tohru Nakashizuka, I. Fang Sun, Renato Valencia, Yunyun Wang, Jess K. Zimmerman, Anthony R. Ives, and S. Joseph Wright. Temporal coexistence mechanisms contribute to the latitudinal gradient in forest diversity. *Nature*, 550(7674):105–108, 2017.

[19] Stephen P Hubell. *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*. Princeton University Press, 2001.

[20] Sean R. Connolly, Terry P. Hughes, and David R. Bellwood. A unified model explains commonness and rarity on coral reefs. *Ecology Letters*, 20(4):477–486, 2017.

[21] Keith Harris, Todd L. Parsons, Umer Z. Ijaz, Leo Lahti, Ian Holmes, and Christopher Quince. Linking Statistical and Ecological Theory: Hubbell's Unified Neutral Theory of Biodiversity as a Hierarchical Dirichlet Process: This paper addresses the issue of a species occupying a specific ecological niche by introducing a new algorithmic model that . In *Proceedings of the IEEE*, 2017.

[22] Anita Narwani, Markos A. Alexandrou, Todd H. Oakley, Ian T. Carroll, and Bradley J. Cardinale. Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. *Ecology Letters*, 16(11):1373–1381, 2013.

[23] Olavi. Renkonen. Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. *Societas zoologica-botanica Fennica Vanamo*, 1938.

[24] Masaaki Morisita. Measuring of Interspecific Association and Similarity Between Communities, 1959.

[25] Stuart H. Hurlbert. The Measurement of Niche Overlap and Some Relatives, 1978.

[26] Peter Chesson. MacArthur's consumer-resource model. *Theoretical Population Biology*, 37(1):26–38, 1990.

[27] Ian T. Carroll, Bradley J. Cardinale, and Roger M. Nisbet. Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology*, 92(5):1157–1165, 2011.

[28] Malyon D. Bimler, Daniel B. Stouffer, Hao Ran Lai, and Margaret M. Mayfield. Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency. *Journal of Ecology*, 106(5):1839–1852, 2018.

[29] Lin Zhao, Quan Guo Zhang, and Da Yong Zhang. Evolution alters ecological mechanisms of coexistence in experimental microcosms. *Functional Ecology*, 30(8):1440–1446, 2016.

[30] Oscar Godoy and Jonathan M. Levine. Phenology effects on invasion success: Insights from coupling field experiments to coexistence theory. *Ecology*, 95(3):726–736, 2014.

[31] Serguei Saavedra, Rudolf P. Rohr, Jordi Bascompte, Oscar Godoy, Nathan J.B. Kraft, and Jonathan M. Levine. A structural approach for understanding multispecies coexistence. *Ecological Monographs*, 87(3):470–486, 2017.

[32] Peter B. Adler, Harmony J. Dalgleish, and Stephen P. Ellner. Forecasting plant community impacts of climate variability and change: When do competitive interactions matter? *Journal of Ecology*, 100(2):478–487, 2012.

[33] Oscar Godoy, Nathan J.B. Kraft, and Jonathan M. Levine. Phylogenetic relatedness and the determinants of competitive outcomes. *Ecology Letters*, 17(7):836–844, 2014.

[34] RM Germain, JT Weir, and Benjamin Gilbert. Species coexistence: macroevolutionary patterns and the contigency of historical interactions. *PRSB*, 283:20160047, 2016.

[35] Po-Ju Ke and Andrew D Letten. Coexistence theory and the frequency dependence of priority effects. *biorXiv*, 2018.

[36] Sebastian J Schreiber, Masato Yamamichi, and Sharon Y Strauss. When rarity has costs : coexistence under positive frequency-dependence and environmental stochasticity. *biorXiv*, (2):1–28, 2017.

[37] Oscar Godoy, Daniel B. Stouffer, Nathan J.B. Kraft, and Jonathan M. Levine. Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences. *Ecology*, 98(5):1193–1200, 2017.

[38] Jacopo Grilli, György Barabás, Matthew J. Michalska-Smith, and Stefano Allesina. Higher-order interactions stabilize dynamics in competitive network models. *Nature*, 548(7666):210–213, 2017.

[39] Michael Turelli. Does environmental variability limit niche overlap? *Proceedings of the National Academy of Sciences of the United States of America*, 75(10):5085–9, 1978.

[40] P. Chesson. Multispecies Competition in Variable Environments. *Theoretical Population Biology*, 45(3):227–276, 1994.

[41] José M. Montoya, Stuart L. Pimm, and Ricard V. Solé. Ecological networks and their fragility. *Nature*, 442(7100):259–264, 2006.