

RESEARCH OUTPUTS / RÉSULTATS DE RECHERCHE

Fitness differences, not niche differences, limit species richness

Spaak, Jurg W.; Carpentier, Camille; Laender, Frederik De

Published in:
bioRxiv

DOI:
[10.1101/823070](https://doi.org/10.1101/823070)

Publication date:
2019

Document Version
Early version, also known as pre-print

[Link to publication](#)

Citation for published version (HARVARD):

Spaak, JW, Carpentier, C & Laender, FD 2019, 'Fitness differences, not niche differences, limit species richness', *bioRxiv*. <https://doi.org/10.1101/823070>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Fitness differences, not niche differences, limit species richness

Jurg W. Spaak^{a,1}, Camille Carpentier^a, and Frederik De Laender^a

^aUniversity of Namur, Institute of Life-Earth-Environment, Namur Center for Complex Systems, 5000 Namur, Rue de Bruxelles 61, Belgium

This manuscript was compiled on October 29, 2019

1 **A key question in ecology is what limits species richness. Co-**
2 **existence theory presents the persistence of species amidst het-**
3 **erospecifics as a balance between niche differences and fitness dif-**
4 **ferences that favour and hamper coexistence, respectively. With**
5 **most applications focusing on species pairs, we know little about**
6 **how niche and fitness differences respond to species richness, i.e.**
7 **what constrains richness most. We present analytical proof that, in**
8 **absence of higher-order interactions, the average fitness difference**
9 **increases with richness, while the average niche difference stays**
10 **constant. Analysis of a simple model with higher-order interactions,**
11 **extensive simulations that relaxed all assumptions, and analyses of**
12 **empirical data, confirmed these results. Our work thus shows that**
13 **fitness differences, not niche difference, limit species richness. Our**
14 **results contribute to the expansion of coexistence theory towards**
15 **multi-species communities.**

niche differences | fitness differences | competition | mutualism | coexistence |
multi-species

1 **E**xplaining nature's biodiversity is a key challenge for sci-
2 ence (1). Coexistence theory predicts species persistence
3 when niche differences overcome fitness differences (\mathcal{N} and \mathcal{F}).
4 \mathcal{N} measures the strength of negative frequency dependency,
5 i.e. whether a species can recover when reduced to small abun-
6 dance. \mathcal{F} measures the intrinsic strength of a species in the
7 absence of niche differences ($\mathcal{N} = 0$), when the species with
8 the highest \mathcal{F} will exclude all other species.

9 Given these two ingredients of coexistence theory, it can
10 be asked what limits species richness: \mathcal{N} becoming too small,
11 or \mathcal{F} becoming too strong, as we pack more species into a
12 community. Available applications of coexistence theory do
13 not address this question. This is because these have typically
14 focused on two-species communities (2, 3), using a variety of
15 experimental and theoretical approaches. \mathcal{N} and \mathcal{F} have been
16 measured in various systems, including annual and perennial
17 plants (4, 5), phytoplankton (6, 7) and bacteria (8), and under
18 different environmental conditions including drought (9–11),
19 biotic soil conditions (12, 13), and water availability (14). In
20 these communities, environmental gradients affect \mathcal{N} and \mathcal{F}
21 (15), phylogenetic distance increases \mathcal{N} and \mathcal{F} (4, 6), and \mathcal{N} is
22 a better predictor for coexistence than \mathcal{F} (7). However, all these
23 studies have been performed on two-species communities and
24 only three studies report \mathcal{N} and \mathcal{F} in communities composed
25 of more than two species (hereafter multi-species communities)
26 (16–18). However, none of these last studies have addressed
27 the question what limits species richness: too low \mathcal{N} , or too
28 high \mathcal{F} .

29 Studying multi-species coexistence is challenging both theo-
30 retically and experimentally. Theoretically speaking, the meth-
31 ods to analyse coexistence via \mathcal{N} and \mathcal{F} in a multi-species
32 community were not available until recently (19–22). Experi-
33 mentally speaking, studying coexistence of multiple species is

resource-demanding. For instance, in the simple case of linear
direct interactions among species (i.e. as in Lotka-Volterra
models) the number of experiments needed to parametrize
the community is quadratic in species richness. Considering
higher order interactions will consequently result in a higher
experimental load. For example, measuring higher order in-
teractions (sensu. (23)) would imply 39 experiments in a three
species community.

It is far from sure if the main results obtained in two-species
communities apply to multi-species communities (17, 23, 24).
Multi-species communities possess at least four complexities
that are absent from two-species communities, and therefore
may affect \mathcal{N} and \mathcal{F} in ways that do not occur in two-species
communities. (1) In a multi-species community multiple in-
teraction types can co-occur. Species richness increases the
number of possible interactions, the number of possible interac-
tion types and the number of combinations of these interaction
types. Several summary metrics exist to understand this vast
quantity of different possible communities (25). (2) Two-species
communities are always fully connected and there's no corre-
lation between interspecific interactions, as there is only one
link between species. In an n -species community there may be
anywhere from $n - 1$ (e.g. food chains) to $\frac{n}{2}(n - 1)$ (e.g. fully
connected competitive network) links and these interspecific
interactions may be positively or negatively correlated (26). (27–
29) have shown that connectance and correlation play a mayor
role in multi-species stability, we therefore expect them to in-
fluence coexistence as well. (3) Higher-order interactions can
make a third species change the interaction between a species
pair. Such higher-order interactions have been found, for exam-
ple, in communities composed of phytoplankton, bacteria, and
ciliates (30). The bacteria coexisted with the phytoplankton
species and with the ciliate, but all three functional groups
did not coexist. The reason was that the phytoplankton inhi-
bited bacterial aggregation, leaving the latter more vulnerable
to predation. (4) A third species may change the dynamics
of two-species communities via indirect effects, even without
changing the interaction between two species. In the classic
text-book example of Rock-Paper-Scissors communities, these
indirect effects can allow three species to coexist via intransi-
tive effects, while no two species can coexist without the third
(31). We will refer to these complexities throughout the text
with (1) Interaction types, (2) Interaction matrix structure, (3)
Higher-order interactions and (4) indirect interactions

While it is known that species in species rich communities

Author Contributions: J.W.S., C.C. and F.D.L. conceived the study. J.W.S. wrote the code and solved the mathematical equations. J.W.S. wrote the first draft, F.D.L. and C.C. contributed to substantially to revisions.

The authors do not declare any conflict of interest

¹To whom correspondence should be addressed. E-mail: jurg.spaakunamur.be

are less probable to coexist (27, 28, 32, 33), we do not know what limits species richness (\mathcal{N} , \mathcal{F} , or a combination of both), nor if this answer depend on the community investigated.

In this paper we therefore investigate what limits multi-species coexistence. More specifically, we ask how \mathcal{N} and \mathcal{F} changes as the number of species in a community increases, and how the additional complexities (1)-(4) influence these changes. We do so using three independent methods. First, we derive equations that quantify how \mathcal{N} and \mathcal{F} respond to species richness in a community with linear interactions and a model containing simple cases of higher order interactions. Second, we performed simulations in which we measured how \mathcal{N} and \mathcal{F} respond to the species richness in communities with more complex models. These simulations were run as a full-factorial virtual experiment, varying direct species interactions (type, correlation, connectance), indirect interactions, and higher order interactions. Third, we searched the literature for empirically measured Lotka-Volterra interaction matrices and computed \mathcal{N} and \mathcal{F} as a response to species richness. All three methods support the same general conclusion: \mathcal{N} are unaffected by species richness while \mathcal{F} increase with higher species richness. Furthermore, these conclusions are independent of the four complexities (1)-(4).

Results

Analytical solutions. We first focus on the linear Lotka-Volterra model without higher order interactions (i.e. $\beta_{ijk} = \gamma_{ijkl} = 0$). For this case, we can compute explicitly (see appendix 1):

$$\mathcal{E}_i^m = \sum_{\alpha_{ij} \neq 0} \mathcal{E}_{ij} \frac{N_j^{-i,*}}{N_j^*} \quad [1]$$

$$\rho_i^m = \frac{\sum_{\alpha_{ij} \neq 0} \rho_{ij} c_j^i N_j^{-i,*}}{\sum_{\alpha_{ij} \neq 0} c_j^i N_j^{-i,*}} \quad [2]$$

where $\mathcal{E}_i^m = 1 - \mathcal{F}_i^m$ and $\rho_i^m = 1 - \mathcal{N}_i^m$ are the fitness equivalence and the niche overlap of species i in the multi-species community (superscript m), \mathcal{E}_{ij} and ρ_{ij} are the fitness equivalence and the niche overlap of species i in the two-species community consisting of species i and j . c_j^i is the conversion factor from species j to species i , $N_j^{-i,*}$ is the equilibrium density of species j in the absence of species i and N_j^* is the equilibrium density of species j in monoculture (see methods). The sum is taken over all species j with which i interacts directly, i.e. $\alpha_{ij} \neq 0$.

Eq. 1 and 2 show three main results. First, \mathcal{E}_i^m is the weighted sum, across all species pairs, of the two-species fitness equivalences \mathcal{E}_{ij} . The sum of the weights $\sum_{j \neq i} \frac{N_j^{-i,*}}{N_j^*}$ is the relative yield total known from biodiversity ecosystem functioning research (34, 35). In case species coexist, which is the focus of the current manuscript, one expects the relative yield total to increase with species richness (19, 36). Hence, the mean and variance of \mathcal{E} (and therefore of \mathcal{F}) in general increase with species richness. Second, ρ_i^m is the weighted average of the two-species niche overlaps ρ_{ij} . Hence, species richness has on average no effect on niche overlap ρ , and consequently neither on \mathcal{N} . Third, the variance of \mathcal{N} decreases with species richness, because $\text{var}(\frac{1}{n} \sum_i X_i) = \frac{1}{n^2} \sum_i \text{var}(X_i)$, i.e. variance decreases with sample size. Since we did not make assumptions about the α_{ij} , these results are independent of them, i.e. the results apply regardless of complexities (1) and (2).

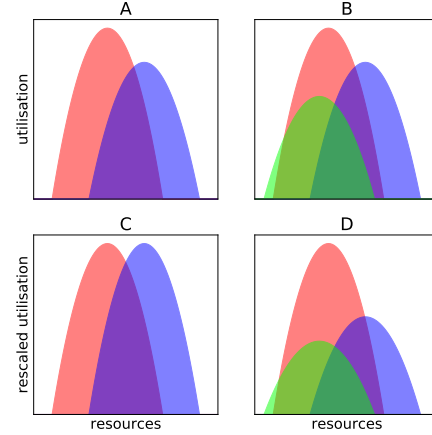


Fig. 1. Illustration of how to compute \mathcal{F} (A,B) and \mathcal{N} (C,D) for two (A,C) and three (B,D) species community. As an illustration, we chose the Mac Arthur resource model in which several species (red, blue and green) consume a resource continuum at different frequencies (e.g. birds with different beak size consuming seeds of different size). All else being equal, \mathcal{F} measures how much resources the focal species consumes, compared to the consumption by its competitors (i.e. $\mathcal{F}_{red}^m = 1 - \frac{\sum \|A_{residents}\|}{\|A_{red}\|}$) (22). To compute \mathcal{N} , the resource consumption of the focal species and all its competitors combined must first be scaled to have the same area, this is done via c_{blue} (i.e. $c_{blue} = \frac{\|A_{blue}\|}{\|A_{red}\|}$) (22). \mathcal{N} is the proportion of red area, not shared with the competitor species, when both areas have been scaled to equal size (i.e. $\mathcal{N}_{red}^m = 1 - \frac{\|A_{red}\| \cap \sum \|A_{residents}\|}{\sum \|A_{residents}\|}$).

That \mathcal{E}_i^m is a weighted sum while ρ_i^m is a weighted average makes intuitive sense when realising that the interaction coefficients α_{ij} can under certain conditions be related to the Mac-Arthur resource competition model (37, 38). Consider three species (noted "red", "blue" and "green" hereafter) that consume a resource continuum at different frequencies (Fig. 1 A). We assume that the species only differ in their resource consumption, not in other parameters such as mortality. We want to compute the \mathcal{N} and \mathcal{F} of the red focal species in presence of the blue (only) or blue and green (combined) competitors. The species with the higher total consumption will have a fitness advantage. Intuitively, one could therefore expect that $\mathcal{E}_{red} \approx \frac{\|A_{blue}\|}{\|A_{red}\|}$, where A_{red} and A_{blue} denote the consumption by the red and the blue species (see fig 1). $\|A_{red}\|$ denotes the total consumption by the red species, i.e. $\|A_{red}\|$ is a real number, while A_{red} is a vector. In a multi-species community, one could therefore expect that $\mathcal{E}_{red}^m \approx \frac{\sum \|A_{residents}\|}{\|A_{red}\|} = \sum \frac{\|A_{residents}\|}{\|A_{red}\|}$ (Fig.1 B). It turns out that the intuition is almost correct; we only have to add different weights to the sum, according to the densities of the species at equilibrium (compare this equation to eq. 1) (22). \mathcal{E}_{red}^m thus increases, and \mathcal{F} therefore becomes more negative, as species richness increases (recall that $\mathcal{F} = 0$ means no fitness differences and more negative \mathcal{F} mean stronger fitness differences).

ρ measures the relative difference in niches, so we must remove differences in total consumption to compute ρ . This is done by rescaling the consumption of both species, such that both consume the same total amount of resources, via the conversion factors $c_{blue} = \frac{\|A_{blue}\|}{\|A_{red}\|} = c_{red}^{-1}$ (note that

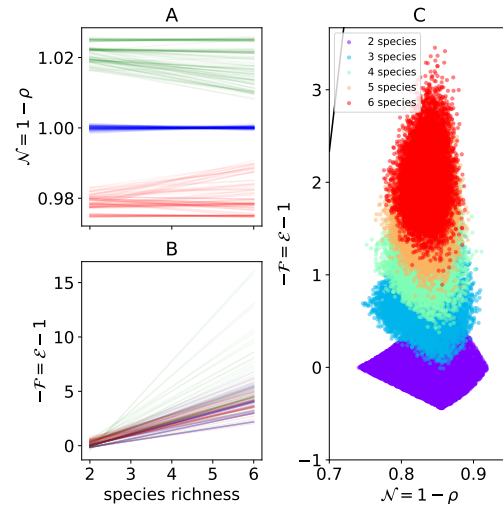
163 $c_{red}^{-1} = \mathcal{E}_{red}$ is a coincidence in this very simple model and
 164 does not hold in general). Intuitively ρ is the proportion
 165 of shared resources between the two species after rescal-
 166 ing, i.e. $\rho = \frac{\|A_{red} \cap (\frac{\|A_{red}\|}{\|A_{blue}\|} A_{blue})\|}{\|A_{red}\| + \frac{\|A_{red}\|}{\|A_{blue}\|} \|A_{blue}\|} = \frac{\|A_{red} \cap A_{blue}\|}{\|A_{red}\| + \|A_{blue}\|}$, where
 167 \cap denotes the intersection of the two consumption vectors
 168 (purple area in Fig. 1 C) (22). In a multi-species commu-
 169 nity, we therefore expect that $\rho_{red}^m \approx \frac{\|A_{red} \cap (A_{green} + A_{blue})\|}{\|A_{red}\| + \|A_{green} + A_{blue}\|} =$
 170 $\frac{\sum (\|A_{residents}\| \cdot \frac{\|A_{red} \cap A_{residents}\|}{\|A_{residents}\|})}{\sum \|A_{residents}\|}$ is a weighted average (Fig. 1 D).
 171 Again this intuition holds, after weighing with species densi-
 172 ties.

173 We can approximate \mathcal{N} and \mathcal{F} in a multi-species community
 174 by using the average interspecific interaction strength $\bar{\alpha}$ (see
 175 appendix 1). This yields $\mathcal{N}_i^m \approx 1 - \bar{\alpha}$ and $\mathcal{F}_i^m \approx 1 - \frac{n-1}{1-(n-2)\bar{\alpha}}$,
 176 from which it is clear that \mathcal{N} is independent of species richness
 177 n and \mathcal{F} is an increasing but saturating function of species
 178 richness. The saturation occurs because the sum of the weights
 179 $\frac{N_i^{-i*}}{N_j^*}$, the relative yield total, will saturate as well in the Lotka-
 180 Volterra model.

181 To investigate the complexity (3) we remove indirect effects.
 182 To remove these, we set $N_j^{-i*} = N_j^*$, i.e. species k does not
 183 affect the density of species j , it only directly affects species i
 184 via $\alpha_{ik} N_k^*$. This will make \mathcal{F} more negative (therefore larger),
 185 as we change the weights of the sum. More importantly, \mathcal{F}
 186 changes from a saturating to a linear response in species rich-
 187 ness, i.e. $\mathcal{F} \approx 1 - (n-1)$ on average. Conversely, removing
 188 indirect effects will not change \mathcal{N} on average, therefore not
 189 altering the response of \mathcal{N} to species richness. This yields
 190 an important result: Indirect effects are purely equalizing as
 191 they do not change stabilisation. Indirect effects thus promote
 192 coexistence (2).

193 We also found an analytical solution for \mathcal{N} and \mathcal{F} as a
 194 function of species richness when higher order effects were
 195 involved (complexity (4)), but only in the simplified case of
 196 constant interspecific interactions and fixed higher-order inter-
 197 actions ($\alpha_{ij} = \bar{\alpha}, \beta_{ijk} = \bar{\beta}, \gamma_{ijkl} = \bar{\gamma}$). In this case, the main
 198 results remained valid: $\mathcal{N}_i^m = 1 - \bar{\alpha}$ and $\mathcal{F}_i^m = 1 - \frac{n-1}{1-(n-2)\bar{\alpha}}$
 199 (see appendix 1).

200 **Full-factorial simulations.** The simulations using random ma-
 201 trices confirm the predictions made by theory. \mathcal{N} is on average
 202 unaffected by species richness and \mathcal{F} increases with species
 203 richness for all parameters settings of the full-factorial simu-
 204 lations (see Fig. 2 A,B). First order interaction strength domi-
 205 nated the effects of species richness on \mathcal{N} . The average of \mathcal{N} ,
 206 $\bar{\mathcal{N}}$, is unaffected by any other factor than first order interaction
 207 strength, i.e. $\bar{\mathcal{N}} = 1 - \bar{\alpha}$. Species richness does not affect \mathcal{N}
 208 (the slope of the linear regressions ranged between -0.005 and
 209 0.003 for all parameter combinations). Variation of \mathcal{N} was only
 210 affected by the first order interaction strength. The variation of
 211 \mathcal{N} decreases with species richness in almost all cases (> 95%).
 212 In the other cases, variation increases only negligibly (the max-
 213 imal slope was 0.0003). Connectance slightly decreased the
 214 negative effect of species richness on variation. The presence of
 215 second order interactions (positive, negative or both) increased
 216 the negative effect of species richness on the variation of \mathcal{N} .
 217 The other factors (correlation, indirect effects, presence of third
 218 order interactions) had no effect on \mathcal{N} or the variation of \mathcal{N} .



219 **Fig. 2.** \mathcal{N} and \mathcal{F} as a function of species richness in simulated communities. A: \mathcal{N} is
 220 unaffected by species richness in general. Each line represents a linear regression of
 221 \mathcal{N} as a function of species richness for one factorial setting of the full-factorial
 222 experiment (see table 1). The color indicates the factor level for first order (direct)
 223 interactions, green indicates positive, blue indicates negative and red indicates mixed
 224 interspecific interactions. B: Species richness, however, makes fitness differences
 225 more negative (i.e. larger). Note the differences in y-scale between panel A and B. C:
 226 Distribution of \mathcal{N} and \mathcal{F} for simulated theoretical competitive communities that are
 227 fully connected, and exhibit first order interactions without correlations, i.e. similar to
 228 the experimental communities (see Fig. 3). Each dot represents \mathcal{N} and \mathcal{F} of one
 229 species in a community composed of 2-6 species (see colour legend). The black line
 230 indicates the persistence line, species below this line are assumed to persist in the
 231 community. Note the inverted y-axis.

232 Multiple factors had effects on \mathcal{F} . First order interactions
 233 affected the mean \mathcal{F} and the effect of species richness on \mathcal{F} as
 234 predicted by our analytical derivation (see eq. 4). High con-
 235 nectance decreased the mean of \mathcal{F} , because the sum in eq. 1
 236 is only taken over species with which the focal species interacts.
 237 Positive correlation of interspecific interactions decreased the
 238 mean \mathcal{F} , because for perfectly correlated interspecific inter-
 239 action strengths we have $\mathcal{F}_{ij} = 0$, negative correlation on the
 240 other hand increased it. Second order interactions increased
 241 the mean of \mathcal{F} when these interactions were positive, but de-
 242 creased them when they were negative. Presence or absence
 243 of third order interactions had very little effect on \mathcal{F} . We illus-
 244 trate how \mathcal{N} and \mathcal{F} values jointly varied with species richness,
 245 using interaction strengths that are representative for experi-
 246 mental communities evaluated in the next section (Fig. 2 C):
 247 $0.08 \leq \alpha_{ij} \leq 0.26, \beta_{ijk} = \gamma_{ijkl} = 0$, no correlation between the
 248 α_{ij} , and maximum connectance.

249 **Literature data.** The results for the real communities reflect
 250 those obtained for the simulated communities. The absolute
 251 values of the slope of the linear regression of \mathcal{N} were small
 252 (< 0.05) for all but 6 datasets. The slope for the overall regres-
 253 sion of \mathcal{N} against species richness (Fig. 3A, black line) was
 254 small(-0.028). \mathcal{F} increased with richness in all but one dataset.
 255 Overall, we conclude that the response of \mathcal{N} and \mathcal{F} to richness
 256 for real communities did not qualitatively differ from that of
 257 randomly generated communities.

258 The empirical data also revealed cases in which coexistence
 259 is possible even though some of the species have negative
 260 \mathcal{N} . This is possible as long as \mathcal{F}_i is sufficiently positive such
 261 that

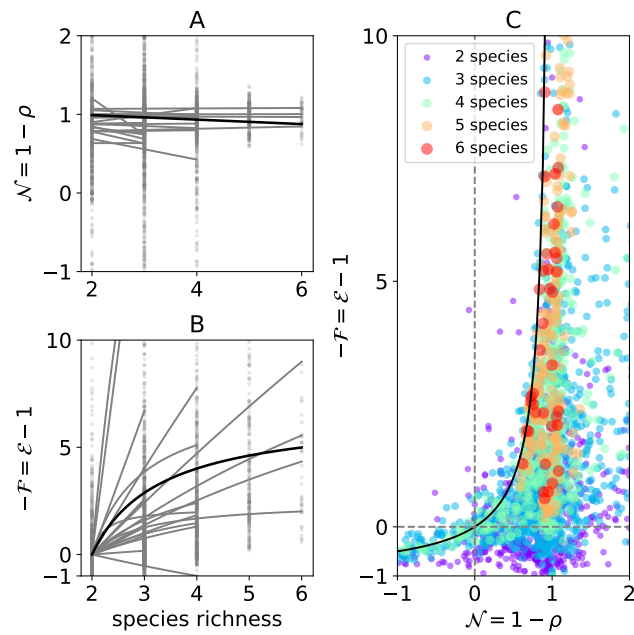


Fig. 3. \mathcal{N} and \mathcal{F} as a function of species richness in empirically measured communities. Each grey line corresponds to a fit of a linear (\mathcal{N}) and saturating (\mathcal{F}) regression model to one dataset. The black line represents a fit through all \mathcal{N} respectively \mathcal{F} values. Grey dots in panel A and B represent the raw \mathcal{N} and \mathcal{F} values. Mutualism, i.e. species having a positive net effect on another, and therefore $\mathcal{N} > 1$ is common in the datasets we found. Axis truncated to show $\sim 95\%$ of all data points.

become to strong for \mathcal{N} .

The results we obtained are consistent throughout the three different methods we chose, i.e. analytical derivations, simulations, and analysis of empirical data. Overall, our results are robust to inclusion or omission of the complexities (1)-(4), and all their combinations. However, some complexities could not be investigated by all methods. Complexity (1), interaction types, are the main drivers of \mathcal{N} and \mathcal{F} : $\mathcal{N} \approx 1 - \bar{\alpha}$ and $\mathcal{F} \approx 1 - \frac{n-1}{1-(n-2)\bar{\alpha}}$. Complexity (2), interaction matrix structure, contains correlation and connectance. Correlation affects \mathcal{N}_i and \mathcal{F}_i indirectly, via its effect on the two-species community \mathcal{N}_{ij} and \mathcal{F}_{ij} . Low connectance decreases the effect of species richness on \mathcal{N} and \mathcal{F} , effectively the number of interactions are relevant for \mathcal{N} and \mathcal{F} in multi-species communities, and not the species richness of a community per se. Complexity (3), higher order interactions, affected \mathcal{F} , but not \mathcal{N} . Positive higher order interactions ($\beta_{ijk} > 0$) increase \mathcal{F} and negative higher order interactions decrease \mathcal{F} . Complexity (4), indirect interactions, also only affected \mathcal{F} , but not \mathcal{N} . Indirect effects decrease \mathcal{F} in competitive communities and increase \mathcal{F} in mutualistic communities.

These results contradict those obtained by (17). Chu et al. (17) found that species richness will decrease \mathcal{N} and will not affect \mathcal{F} . The use of different definitions for \mathcal{N} and \mathcal{F} explains this difference (19). Indeed, applying the same definition to our data reproduces the results found by (17) (\mathcal{N} is affected by species richness, while \mathcal{F} is not (see Appendix 3) and which seemingly contradict our main findings. However, we argue that our results provide a more accurate account of how \mathcal{N} and \mathcal{F} limit multi-species coexistence because of the following reasons: 1. The definition of (22) does not only consider negative frequency dependence, but also positive frequency dependence and facilitation. The definition of (19) can only be computed for communities with negative frequency dependence, which precludes the analysis of 75% of the empirical data and 67% of the simulated data presented here. 2. The \mathcal{N} and \mathcal{F} as defined by (22) clearly link to persistence of a species via the equation $-\mathcal{F} \leq \frac{\mathcal{N}}{1-\mathcal{N}}$. Again, this is not the case for the definition by (19) in multi-species-communities. Since we explicitly ask whether \mathcal{N} or \mathcal{F} is more limiting for coexistence in multi-species communities, the definition of (19) can not be used. 3. (22) show that \mathcal{N} is biologically intuitive as it measures the amount of shared resources in a large class of resource competition models. Fig.1 extends this intuitive explanation to multi-species communities. (19) has so far only been linked to the Mac-Arthur resource model and it is not clear how it relates to more complex resource competition models.

Limitations. The available experimental data only represented fully connected communities, with no correlation (complexity (2)) among interactions and, most notably, did not contain cases of higher order interactions (complexity (3)). We do therefore not know whether the parameter values used to describe these higher-order interactions are realistic or whether more realistic values exist that would lead to different results. The available experimental data were biased towards fully connected, competitive communities of terrestrial plants with relatively low species richness. Our simulations suggest that our conclusions hold for other networks as well, but we were not able to back up this claim with empirical data. Computing

that $\mathcal{F}_i \geq \frac{-\mathcal{N}_i}{1-\mathcal{N}_i}$. A total of 95 (4.1%) communities were found with species persisting despite having negative \mathcal{N} , indicating that this is not a rare phenomena. Negative \mathcal{N} are typically attributed to priority effects, which prelude coexistence (39, 40). Coexistence with negative \mathcal{N} is possible in multi-species communities, because not all species have negative \mathcal{N} , but only a few.

Discussion

The potential for coexistence decreases with species richness (24, 27, 32, 33). We explained this result using the key concepts of modern coexistence theory, i.e. \mathcal{N} and \mathcal{F} . We found that species richness does, on average, not affect niche differences but does increase fitness differences. Thus, it are interspecific differences that limit the coexistence of multiple species, rather than interspecific similarities. These results are based on three independent methods: analytical computation, numerical simulations and metanalysis of experimental data. The \mathcal{F} of a species increases with species richness, as \mathcal{F} measures the fitness of a species compared to the combined fitness of all other species. In multi-species communities, most species will therefore have negative \mathcal{F} , as rarely one species will have higher fitness than all other species combined.

The \mathcal{N} of a species measures the proportion of limiting factors, e.g. resources, that are limiting to other species as well. Increasing species richness increases the amount of limiting factors shared, but also the amount of limiting factors that are not shared. The proportion of shared limiting factors is therefore unaffected on average. Species-rich communities are therefore less likely to coexist (all else being equal), as \mathcal{F}

337 \mathcal{N} and \mathcal{F} on a larger collection of real networks would help
338 to refine our understanding of this process. However, obtain-
339 ing the full interaction matrix for species rich communities
340 is still challenging. Qualitative interaction data are not suffi-
341 cient to compute \mathcal{N} and \mathcal{F} . To obtain quantitative data, one
342 uses frequency of interaction between species (e.g. number
343 of visits of a pollinator on a plant) as a proxy for interaction
344 strength. The robustness of this approach, however, still needs
345 to be tested (41). Other methods consist of estimating interac-
346 tion strength based on, for example, biomass (42), mass ratio
347 (43) or production and consumption rates of species (44, 45).
348 These different methods have different assumptions and may
349 therefore influence the resulting matrix estimate (46).

350 Given these limitations, one can ask to what extent our
351 conclusions will hold in other community models. In com-
352 munities where species richness increases total abundance,
353 which is often the case (36, 47), we expect species richness to
354 increase \mathcal{F} as well (make it more negative), as the no-niche
355 growth rate will be more negative. Conversely, in communities
356 where species richness decreases total abundance we expect
357 the opposite. Similarly, in competitive communities indirect ef-
358 fects decrease total abundance and therefore also \mathcal{F} . However,
359 in mutualistic communities indirect effects will increase total
360 abundance and therefore also \mathcal{F} . It is less clear how species
361 richness will affect \mathcal{N} in models not explored in the current
362 paper. \mathcal{N} depends on the invasion growth rate and the no-
363 niche growth rates, which both depend on the species richness
364 and total abundance. Whether \mathcal{N} increases or decreases with
365 species richness will therefore depend on how species richness
366 affects these growth rates.

367 **New insights.** Our results yield three new insights, other than
368 the main result on how \mathcal{N} and \mathcal{F} varies with species richness.
369 A first insight is that negative \mathcal{N} do not necessarily preclude
370 coexistence. Negative \mathcal{N} have been attributed to priority effects
371 and therefore were viewed as precluding coexistence (39, 40).
372 Our framework confirms this finding for the case of competi-
373 tive two-species communities, where the species with $\mathcal{F} < 0$
374 will not be able to persist (22). However, in contrast to species
375 in two-species communities, species in multi-species commu-
376 nities will not all have the same \mathcal{N} . This implies that a species
377 with negative \mathcal{N} and low \mathcal{F} can coexist with other species that
378 have high \mathcal{N} and negative \mathcal{F} . Consequently, multiple species
379 can have negative \mathcal{N} in a multi-species communities and still
380 persist. For example, we found six three-species communities
381 in which all but one species had negative \mathcal{N} . In general, we
382 argue that it would be theoretically possible to construct a
383 community model in which all species have negative \mathcal{N} and
384 coexist. The kind of model and how it should be parametrized
385 remains to be examined, however.

386 A second insight is that indirect effects, and to some extent
387 higher-order effects, are equalising. While direct interaction
388 affect both \mathcal{N} and \mathcal{F} , indirect and higher order effects mainly
389 affect \mathcal{F} and should therefore be seen as equalizing effects
390 (2). Indirect interactions and higher order interactions alone,
391 i.e. in the absence of any niche differentiation via first order
392 interactions, will therefore not be able to sustain coexistence,
393 as equalizing effects cannot sustain multiple species in the ab-
394 sence of stabilizing effects (2, 48). This is confirmed by (24) and
395 (49) who found that intransitivity in annual grassland commu-
396 nities, in the absence of \mathcal{N} , is not able to sustain coexistence.
397 They may however promote coexistence in the presence of

some \mathcal{N} , by reducing \mathcal{F} , just as other equalizing mechanisms
do.

A third and main insight is that one can infer \mathcal{N} and \mathcal{F}
in multi-species communities from \mathcal{N} and \mathcal{F} measured in
pairwise interaction experiments. If one measures \mathcal{N} and \mathcal{F}
for each two-species sub-community of an n species commu-
nity, which is typically done (4, 6, 7, 18), one can estimate
 $\mathcal{N}_i \approx \frac{\sum_j \mathcal{N}_{ij}}{(n-1)}$. With one additional multi-species experiment
to estimate the relative yield RY_i we obtain an estimation of
 $\mathcal{F}_i \approx 1 - \sum_j (1 - \mathcal{F}_j) \cdot \text{RY}_j$ as well. This indicates that two-
species experiments are sufficient to predict \mathcal{N} and \mathcal{F} in multi-
species communities.

One of the key questions in community ecology is whether
 \mathcal{N} are strong enough to overcome \mathcal{F} and allow coexistence.
Often they are found to be not only sufficiently strong, but
much stronger than needed (17, 50). The present results offer a
potential explanation for this observation. That is, \mathcal{N} not only
need to be sufficiently strong to overcome \mathcal{F} of one or few
competitors, but sufficiently strong to overcome \mathcal{F} of the entire
resident community, as \mathcal{N} is independent of species richness.
Our results therefore allow asking the more general question
how many species one can pack in a community, given \mathcal{N} that
are invariant of species richness.

Methods

Model description. We use a generalized Lotka-Volterra model
with n species containing higher order interactions:

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i \left(1 - \sum_j \alpha_{ij} N_j \left(1 + \sum_k \beta_{ijk} N_k \left(1 + \sum_l \gamma_{ijkl} N_l \right) \right) \right) \quad [3]$$

Where N_i is the density of the focal species i . r_i is the mono-
culture growth rate at low density. α_{ij} , β_{ijk} and γ_{ijkl} are first
or linear, second, and third-order species interactions, respec-
tively. A positive α_{ij} indicates a *negative* interaction between
species i and j such as competition or predation. Negative α_{ij}
on the other hand indicate positive interactions such as facili-
tation or consumption. If β_{ijk} is positive or negative, species
 k will intensify or weaken the relationship between species i
and j , respectively (second order interaction). Similarly, when-
ever γ_{ijkl} differs from zero (third order interaction), species l
can influence the second-order interaction. Throughout the
manuscript, we take $\alpha_{ii} = 1$.

There exist five different definitions to quantify \mathcal{N} and \mathcal{F} in
multi-species communities (19–22, 51). The definitions of (21)
does not apply to the selected model. (51) was developed for
environmental or spatial fluctuations, which we don't consider
here. (20) and (19) do apply to the selected model. However,
 \mathcal{N} and \mathcal{F} as computed by these two methods allow inter-
ference about coexistence only in two-species communities,
not in multi-species communities. That is, two different multi-
species communities may have identical \mathcal{N} and \mathcal{F} but different
outcomes of coexistence in both. Since we here ask whether
coexistence in multi-species communities is driven by \mathcal{N} or \mathcal{F} ,
these two methods are therefore not suitable. Consequently,
we computed \mathcal{N} and \mathcal{F} as defined by (22):

$$\mathcal{N}_i = \frac{f_i(0, N^{-i,*}) - f_i(\sum_{j \neq i} c_j^i N_j^{-i,*}, \mathbf{0})}{f_i(0, \mathbf{0}) - f_i(\sum_{j \neq i} c_j^i N_j^{-i,*}, \mathbf{0})} \quad [4]$$

$$\mathcal{F}_i = \frac{f_i(\sum_{j \neq i} c_j^i N_j^{-i,*}, \mathbf{0})}{f_i(0, \mathbf{0})} \quad [5]$$

Where f_i is the per capita growth rate of species i , i.e. $f_i(N_i, N^{-i}) = \frac{1}{N_i} \frac{dN_i}{dt}$. The first argument of $f_i(N_i)$ is the density of the focal species i , the second argument (N^{-i}) is a vector of length containing the densities of the $n - 1$ non-focal species. $N^{-i,*}$ is the equilibrium density of each non-focal species of the community in the absence of species i . c_j^i , the conversion factor of species j to species i , equates the total dependencies on limiting factor for species i and j (see fig. 1). \mathcal{N}_i and \mathcal{F}_i are species specific properties, i.e. in general we have $\mathcal{N}_i \neq \mathcal{N}_j$ and $\mathcal{F}_i \neq \mathcal{F}_j$ in multi-species communities. We introduce niche overlap $\rho = 1 - \mathcal{N}$ and fitness equivalence $\mathcal{E} = 1 - \mathcal{F}$ for simpler interpretation of the results.

Analyses and Simulations. We first examined analytically how \mathcal{N} and \mathcal{F} change with species richness. We found a generic solution for first order interactions and for a simplified case of higher order interactions. This simplification consisted of constant interspecific interactions ($i \neq j \Rightarrow \alpha_{ij} = \alpha$) and constant higher order interactions ($\beta_{ijk} = \beta, \gamma_{ijkl} = \gamma$). These analytical results allowed us to investigate the effects of the complexities (1), (2), (4) and partially (3).

Second, we designed a full-factorial virtual experiment in which we simulated \mathcal{N} and \mathcal{F} for a wide range of different communities (see table 1). The factors were (i) first order interaction type (competitive, mutualistic or both, i.e. $\alpha_{ij} > 0, < 0$ or no restriction). (ii) Connectance of the interspecific interaction ($c \in \{1, \frac{4}{5}, \frac{2}{3}\}$). (iii) Correlation between the interspecific interaction ($\rho(\alpha_{ij}, \alpha_{ji}) = \rho_{ij}(\beta_{ijk}, \beta_{jik}) = \rho_{ij}(\gamma_{ijkl}, \gamma_{jikl}) \in \{-1, 0, 1\}$). (iv) Inclusion of indirect effects. To exclude indirect effects we set equilibrium densities of resident species to their monoculture equilibrium density. (v) Second order interaction type ($\beta_{ijk} < 0, > 0$, no restriction, absent). (vi) Presence of third order interaction type ($\gamma_{ijkl} = 0$ or $\gamma_{ijkl} \neq 0$).

This leads to a total of $3 \cdot 3 \cdot 3 \cdot 2 \cdot 4 \cdot 2 = 432$ parameter settings. We ran 1000 repetitions for each species richness level ($2 \leq n \leq 6$), leading to a total of $432 \cdot 5 \cdot 1000 = 2'160'000$ simulations. To compute \mathcal{N} and \mathcal{F} we chose the magnitude of the interaction strength such that all communities and sub-communities will coexist (i.e. $|\alpha| \leq 0.05, |\beta| \leq 0.05, |\gamma| \leq 0.05$). In all simulations, the non-zero values of the interaction strength were uniformly distributed in their respective range (i.e. $\alpha \in [0, 0.05], [-0.05, 0]$ or $[-0.05, 0.05]$). For each parameter setting we investigated the effect of species richness ($2 \leq n \leq 6$) on \mathcal{N} and \mathcal{F} . We fitted linear regressions to assess the effect of species richness on \mathcal{N} , variation of \mathcal{N} within a community, \mathcal{F} and variation of \mathcal{F} with in a community. As a measure of variation we take the inter-quartile range, as it is a outlier robust equivalent to the variance. We report the effect of species richness (slope of linear regression) and the effect of the parameter combinations (intercept of linear regression) on these parameters. With this approach we were able to investigate the effects of all complexities (1)-(4).

Literature data. We found three review papers of multi-species Lotka-Volterra interaction matrices (5, 52, 53), representing a total of 33 interaction matrices, ranging from 3 to 9 species, and containing 29 plant, 2 phytoplankton, 1 zooplankton and 1 ciliate communities. We normalized all these data such that $\alpha_{ii} = 1$. The interaction matrices were obtained through pairwise experiments, measuring the interspecific effect of one species on the other. For each multi-species community we constructed all possible sub-communities with at least two species, leading to a total of 2544 communities that varied in species richness from 2 to 9. We excluded all communities in which not all interaction strengths were available, leading to 2296 communities. For 1376 communities \mathcal{N} and \mathcal{F} could not be computed because, like any method seeking to quantify frequency dependence, \mathcal{N} and \mathcal{F} is based on invasion analysis: the capacity of an invader to grow with the other species at their non-zero equilibrium. For this the invasion growth rate of each species must be computed, the per capita growth rate $f_i(0, N_j^{-i,*})$ when the focal species i is absent (mathematically equal 0) and the other species at their equilibrium density $N^{-i,*}$. \mathcal{N} and \mathcal{F} can thus only be obtained for communities where each subcommunity (the community without the invading species) coexists stably. We computed \mathcal{N} and \mathcal{F} for a total of 920 communities, the species of 722 of these communities were able to coexist. Species of 46 additional communities did coexist, but did not allow invasion analysis, hence we were not able to compute \mathcal{N} and \mathcal{F} .

We were able to compute \mathcal{N} and \mathcal{F} for about 40% of the real communities. While we could compute \mathcal{N} and \mathcal{F} for all two-species communities, we were able to compute only for 3% of six-species communities. We computed \mathcal{N} and \mathcal{F} for about 94% of all communities in which species coexist, in the remaining communities invasion analysis was not possible. In these \mathcal{N} and \mathcal{F} correctly predicted coexistence, indicating that \mathcal{N} and \mathcal{F} as proposed by (22) is a useful tool to analyse multi-species coexistence. However, for only about 13% of the communities in which species don't coexist we were able to compute \mathcal{N} and \mathcal{F} . We were able to compute \mathcal{N} and \mathcal{F} in these communities because all species in all sub communities coexisted, not however the species in the community as a whole. For a detailed version including numbers of communities per species richness, see appendix 2.

For each interaction matrix obtained from the literature we computed \mathcal{N} and \mathcal{F} as mentioned above. We fit a linear response of \mathcal{N} as a function of species richness per interaction matrix from the literature. The data contained many outliers, which skewed the results of our linear regressions. We therefore used a Theil-Sen estimator for the slope, which is more robust to outliers than linear regression based on least squares (54). We fit (using least squares) a saturating function $\mathcal{F} = \frac{n-2}{(n-2)+H}$ for the fitness differences. This saturating response was chosen for \mathcal{F} , because our analytical results suggest a saturating response. We additionally fitted a regression line through all communities.

With this approach, we were able to investigate the effects of the complexities (1) and (4). The experimental protocol to obtain the interaction matrix does not allow detecting higher order interactions, these are therefore by definition absent from the experimental data. We did not find any data on multi-species communities including higher order interactions (complexity (3)). We did not investigate the effects of con-

Factor	Parameter	Levels	Interpretation	Complexity investigated
Interaction type 1st order	α_{ij}	> 0 < 0 no restriction	competition mutualism mixed	(1)
Connectance	$P(\alpha_{ij} \neq 0)$	$1, \frac{4}{5}, \frac{2}{3}$		(2)
Interaction correlation	$\text{cor}(\alpha_{ij}, \alpha_{ji})$ $\text{cor}_{ij}(\beta_{ijk}, \beta_{jik})$ $\text{cor}_{ij}(\gamma_{ijkl}, \gamma_{jikl})$	1 0 -1	equal unrelated opposite	(2)
Presence of indirect effects		Yes No	absent present	(3)
Interaction type 2nd order	β_{ijk}	> 0 < 0 no restriction	intensify weaken mixed	(1) and (4)
interaction type 3rd order	γ_{ijkl}	$\neq 0$ $= 0$	present absent	(4)

Table 1. Design of full factorial virtual experimental.

nectance, because almost all interaction matrices were fully connected (complexity (2)).

1. Hutchinson GE (1957) Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22(0):415–427.
2. Chesson P (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology, Evolution, and Systematics* 31.
3. Letten AD, Ke PJ, Fukami T (2017) Linking modern coexistence theory and contemporary niche theory. *Ecological Monographs* 87(2):161–177.
4. Godoy O, Levine JM (2014) Phenology effects on invasion success: Insights from coupling field experiments to coexistence theory. *Ecology* 95(3):726–736.
5. Adler PB, et al. (2018) Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters* 21(9):1319–1329.
6. Gallego I, Venail P, Ibelings BW (2019) Size differences predict niche and relative fitness differences between phytoplankton species but not their coexistence. *ISME Journal*.
7. Narwani A, Alexandrou MA, Oakley TH, Carroll IT, Cardinale BJ (2013) Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. *Ecology Letters* 16(11):1373–1381.
8. Zhao L, Zhang QG, Zhang DY (2016) Evolution alters ecological mechanisms of coexistence in experimental microcosms. *Functional Ecology* 30(8):1440–1446.
9. Bimler MB, Stouffer DB, Lai HR, Mayfield MM (2018) Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency. *Journal of Ecology* 106(5):1839–1852.
10. Napier JD, Mordecai EA, Heckman RW (2016) The role of drought- and disturbance-mediated competition in shaping community responses to varied environments. *Oecologia* 181(2):621–632.
11. Matías L, Godoy O, Gómez-Aparicio L, Pérez-Ramos IM (2018) An experimental extreme drought reduces the likelihood of species to coexist despite increasing intransitivity in competitive networks. *Journal of Ecology* 106(3):826–837.
12. Lanuza JB, Bartomeus I, Godoy O (2018) Opposing effects of floral visitors and soil conditions on the determinants of competitive outcomes maintain species diversity in heterogeneous landscapes. *Ecology Letters* 21(6):865–874.
13. Cardinaux A, Hart SP, Alexander JM (2018) Do soil biota influence the outcome of novel interactions between plant competitors? *Journal of Ecology* 106(5):1853–1863.
14. Wainwright CE, HilleRisLambers J, Lai HR, Loy X, Mayfield MM (2018) Distinct responses of niche and fitness differences to water availability underlie variable coexistence outcomes in semi-arid annual plant communities. *Journal of Ecology* (July):1–14.
15. Letten AD, Dhani MK, Ke PJ, Fukami T (2018) Species coexistence through simultaneous fluctuation-dependent mechanisms. *Proceedings of the National Academy of Sciences of the United States of America* 115(26):6745–6750.
16. Veresoglou SD, Rillig MC, Johnson D (2018) Responsiveness of plants to mycorrhiza regulates coexistence. *Journal of Ecology* 106(5):1864–1875.
17. Chu C, Adler PB (2015) Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. *Ecological Monographs* 85(3):373–392.
18. Petry WK, Kandlikar GS, Kraft NJ, Godoy O, Levine JM (2018) A competition–defence trade-off both promotes and weakens coexistence in an annual plant community. *Journal of Ecology* 106(5):1806–1818.
19. Carroll IT, Cardinale BJ, Nisbet RM (2011) Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology* 92(5):1157–1165.
20. Saavedra S, et al. (2017) A structural approach for understanding multispecies coexistence. *Ecological Monographs* 87(3):470–486.
21. Carmel Y, et al. (2017) Using exclusion rate to unify niche and neutral perspectives on coexistence. *Oikos* 126(10):1451–1458.
22. Spaak JW, De Laender F (2018) A unified definition of niche and fitness differences. *bioRxiv* p. 482703.
23. Letten AD, Stouffer DB (2019) The mechanistic basis for higher-order interactions and non-additivity in competitive communities. *Ecology Letters* 22(3):423–436.

24. Godoy O, Stouffer DB, Kraft NJ, Levine JM (2017) Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences. *Ecology* 98(5):1193–1200.
25. Landi P, Minoarivelo HO, Brännström Å, Hui C, Dieckmann U (2018) Complexity and stability of ecological networks: a review of the theory. *Population Ecology* 60(4):319–345.
26. Barabás G, Michalska-Smith MJ, Allesina S (2016) The effect of intra- and interspecific competition on coexistence in multispecies communities. *American Naturalist* 188(1):E1–E12.
27. May RM (1972) Will a large complex system be stable? *Nature* 238(672):413–414.
28. Allesina S, Tang S (2012) Stability criteria for complex ecosystems. *Nature* 483(7388):205–208.
29. Allesina S, Tang S (2015) The stability–complexity relationship at age 40: a random matrix perspective. *Population Ecology* 57(1):63–75.
30. Mickalide H, Kuehn S (2019) Higher-order interaction inhibits bacterial invasion of a phototroph-predator microbial community. *bioRxiv* p. 564260.
31. Grilli J, Barabás G, Michalska-Smith MJ, Allesina S (2017) Higher-order interactions stabilize dynamics in competitive network models. *Nature* 548(7666):210–213.
32. Goh B, Jennings L (1977) No Feasibility and stability in randomly assembled Lotka-Volterra models. *Ecological Modelling* 3(2).
33. Serván CA, Capitán JA, Grilli J, Morrison KE, Allesina S (2018) Coexistence of many species in random ecosystems. *Nature Ecology and Evolution* 2(8):1237–1242.
34. Hector A, Loreau M (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412(July):72–76.
35. Fox JW (2005) Interpreting the ‘selection effect’ of biodiversity on ecosystem function. *Ecology Letters* 8:846–856.
36. Loreau M (2004) Does functional redundancy exist? *Oikos* 104(3):606–611.
37. Chesson P (1990) MacArthur’s consumer-resource model. *Theoretical Population Biology* 37(1):26–38.
38. MacArthur R (1970) Species packing and competitive equilibrium for many species. *Theoretical Population Biology* 1(1):1–11.
39. Ke PJ, Letten AD (2018) Coexistence theory and the frequency dependence of priority effects. *bioRxiv*.
40. Fukami T, Mordecai EA, Ostling A (2016) A framework for priority effects. *Journal of Vegetation Science* 27(1):655–657.
41. García-Callejas D, Molowny-Horas R, Araújo MB (2018) Multiple interactions networks: towards more realistic descriptions of the web of life. *Oikos* 127(1):5–22.
42. Moore JC, De Ruiter PC, Hunt HW, Coleman DC, Freckman DW (1996) Microcosms and soil ecology: Critical linkages between field studies and modelling food webs. *Ecology* 77(3):694–705.
43. Emmerson MC, Raffaelli D (2004) Predator-prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology* 73(3):399–409.
44. Christens V., D. P (1992) ECOPATH II - a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61(3-4):169–185.
45. Jacquet C, et al. (2016) No complexity-stability relationship in empirical ecosystems. *Nature Communications* 7:1–8.
46. Carrara F, Giometto A, Seymour M, Rinaldo A, Altermatt F (2015) Inferring species interactions in ecological communities: A comparison of methods at different levels of complexity. *Methods in Ecology and Evolution* 6(8):895–906.
47. Turnbull LA, Levine JM, Loreau M, Hector A (2013) Coexistence, niches and biodiversity effects on ecosystem functioning. *Ecology Letters* 16(SUPPL.1):116–127.
48. Chesson P (1994) Multispecies Competition in Variable Environments. *Theoretical Population Biology* 45(3):227–276.
49. Gallien L, Zimmermann NE, Levine JM, Adler PB (2017) The effects of intransitive competition on coexistence. *Ecology Letters* 20(7):791–800.
50. Levine JM, HilleRisLambers J (2009) The importance of niches for the maintenance of species diversity. *Nature* 461(7261):254–257.
51. Chesson P (2003) Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. *Theoretical Population Biology* 64(3):345–357.
52. Fort H (2018) On predicting species yields in multispecies communities: Quantifying the accuracy of the linear Lotka-Volterra generalized model. *Ecological Modelling* 387(September):154–162.
53. Keddy PA, Shipley B (1989) Competitive hierarchies in herb plant communities.
54. Sen PK (1968) Estimates of the Regression Coefficient Based on Kendall’s Tau. *Journal of the American Statistical Association* 63(324):1379–1389.