The feasibility and stability of large complex biological networks: a random matrix approach

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Abstract

In his theoretical work of the 70's, Robert May introduced a Random Matrix Theory (RMT) approach for studying the stability of large complex biological systems. Unlike the established paradigm, May demonstrated that complexity leads to instability in generic models of biological networks. The RMT approach has since similarly been applied in many disciplines. Central to the approach is the famous "circular law" that describes the eigenvalue distribution of an important class of random matrices. However the "circular law" generally does not apply for ecological and biological systems in which density-dependence (DD) operates. Here we directly determine the far more complicated eigenvalue distributions of complex DD systems. A simple mathematical solution falls out, that allows us to explore the connection between feasible systems (i.e., having all equilibrium populations positive) and stability. In particular, for these RMT systems, almost all feasible systems are stable. The degree of stability, or resilience, is shown to depend on the minimum equilibrium population, and not directly on factors such as network topology.

Introduction

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32   Network models have become indispensable tools for helping understand the biological
33   processes responsible for the stability and sustainability of biological systems[1-18]. Intuitively, rich
34   highly interconnected biological networks are expected to be the most stable, and are thus likely
35   to better withstand the loss of a link, or to cope in the presence of external environmental
36   perturbations. In the 70's, May[1,2] exploited random matrix theory (RMT), and the "circular law"
37   for matrix eigenvalue distributions, to challenge this paradigm. He demonstrated that more
38   complex and connected biological systems are in fact more fragile, and less likely to be stable, in
39   terms of their ability to recover after some small external perturbation. Since then, the RMT
40   framework has proved extremely useful for identifying those factors that beget stability in large
41   ecological communities of randomly interacting species[5-15]. Moreover, in recent years, the
42   modeling approach has successfully spread to other disciplines, ranging from systems biology,
43   neurosciences, through to atomic physics, wireless, finance and banking, making this an exciting
44   and vibrant contemporary research discipline[16-18].

45   Here I re-examine similar issues of stability versus complexity, while using a better
46   suited formulation of a biological system's "community matrix" -- one that explicitly allows for
47   the standard textbook assumption of density-dependent (DD) growth[2,19,20]. Such growth proves
48   to be the rule rather than the exception for many biological processes, yet surprisingly, very little
49   is known about their stability properties. In principal, May's conclusions are not automatically
50   translatable to DD systems. As we shall see, the "circular law" which sits at the foundation of
51   May's analysis, and governs the eigenvalue distribution of random matrices, generally does not
52   hold for DD systems. The problem has resurfaced in recent prominent studies of ecological
53   networks[6].

54   In this paper we develop new methods to predict eigenvalue distributions of large
55   complex DD systems. In the process, the analysis leads to and justifies new conclusions about
56   the currently topical constraint of *feasibility*[6,7,10,15]. Feasibility requires that all equilibrium
57   populations of a system are positive, a characteristic feature that is generally to be expected for
58   any persistent system. There have been numerous reports in the literature of a strong association
59   between feasibility of DD systems and stability, similar to Roberts (1974) who found that almost
60   all feasible model systems are stable (see also Refs.10-12).

61

62   **Robert May's model of large complex systems:** It is helpful to first recall the original
63   argument of May[1]. For an *n*-species community, let us suppose that the *i*'th species has
64   abundance at time *t* given by $N_i(t) = N_i^* + x_i(t)$. Here N_i^* is the abundance at equilibrium (the
65   symbol * indicating equilibrium), and $x_i(t)$ its perturbation from the equilibrium value. The
66   dynamics of the populations are assumed to follow some complex nonlinear differential
67   equation, which when linearized around equilibrium is of the form:

68
$$\frac{d\mathbf{x}}{dt} = \mathbf{A}\,\mathbf{x} \quad . \tag{1}$$

69   The vector $\mathbf{x} = (x_i)$ contains the population disturbances x_i , in terms of their perturbation from
70   equilibrium, while the element a_{ij} of the "community matrix" $\mathbf{A}$ represents the effect species-*j*
71   has on the growth of species-*i* when close to equilibrium. A cooperative effect implies $a_{ij} > 0$,
72   while a negative effect is just the opposite with $a_{ij} < 0$. The self-interactions between species
73   are all scaled such that $a_{ii} = -1$.
74

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75   May[1] studied communities under the limited *"neutral interaction"* assumption where
76 interspecific interactions are equally positive as negative, and their expected or average value is
77 zero i.e., E(a_{ij})=0. Environmental fluctuations are assumed to perturb the interaction strengths,
78 so that for the basic "neutral interaction" model, $\mathbf{A} = -\mathbf{I} + \mathbf{B}$, where $\mathbf{I}$ is the identity matrix and
79 $\mathbf{B}$ is a random matrix with coefficients having mean zero and variance Var(b_{ij})=σ^2. Finally, to
80 model connectance of the interaction network, a proportion $(1 - C)$ of randomly chosen
81 interactions a_{ij} are set to zero, leaving a proportion C nonzero.

82   More formally, we are interested in the "local stability" of biological models, which
83 guarantees that a system will return to equilibrium after a "small" population perturbation.
84 Unless otherwise stated, the paper will be concerned exclusively with local stability. A major
85 achievement of May[1] was to demonstrate that eqn.1 is locally stable for the neutral interaction
86 model, if the interaction disturbances are "not too large," namely if:

87 $$\boldsymbol{\gamma} < 1 \text{ ,} \qquad \text{where } \gamma = \sqrt{nC}\ \sigma, \qquad (2)$$

88 and unstable otherwise. The larger the number of species *n*, the sharper the transition from
89 stability to instability at $\boldsymbol{\gamma} = 1$. This is visualised in Fig.1a which plots the percentage of
90 random matrices that are locally stable as a function of disturbance $\boldsymbol{\gamma}$. In terms of model
91 parameters, the threshold criterion means that if either *n*, σ or *C* become too large, the system
92 will transition into an unstable regime. With this simple but powerful argument, May
93 demonstrated the fragility of large complex and highly connected systems.
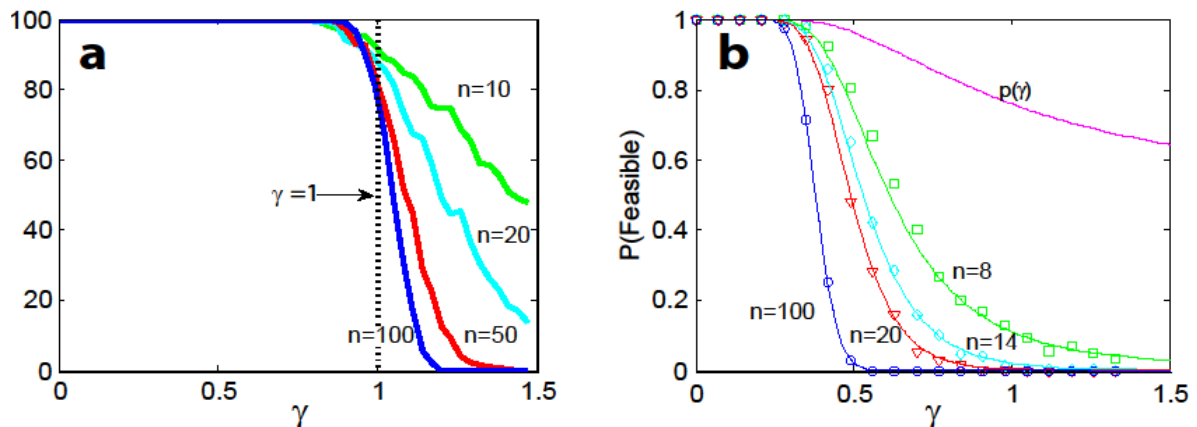
94
95 **Fig 1.** **a)** Percentage of locally stable interaction matrices **A** as a function of disturbance γ in an
96 ensemble of 500 matrices for different community-sizes *n=10,20,50,100*. May's stability threshold sits at
97 $\gamma = 1$. **b)**. The probability of feasibility, *P*(Feasible), as a function of disturbance γ, for *n*-species
98 competition with different community sizes *n=1,8,14,20,100*. Each probability marked by a square, circle,
99 etc is the proportion of feasible systems in 500 runs of eqn.9. Analytical predictions from eqn.12. Figure
100 from Stone (1988, 2016).

101

102 **Results**

3

103   **The eigenvalue distribution of the community matrix S = DA:** Theoretical ecologists study
104   the eigenvalues (λ_i) of the community matrix **A** to determine local stability[2]. The theory
105   underpinning the above elegant stability criterion relies on the "circular law" which is a central
106   result in RMT. In simple terms, it states that the n eigenvalues λ_i of the random matrix **A** are
107   distributed uniformly in a circle with radius γ in the complex plane, and centred at (-1,0) on the
108   real axis as shown in Fig.2a (see Ref.1). In this paper, it is often of interest to study the
109   properties of each new matrix **A**, as γ is increased incrementally from zero. If the radius is
110   increased to the point where it exceeds $\gamma=1$, the eigenvalues of **A** populate the right-hand-side
111   (RHS) of the complex plane indicating that at least one eigenvalue has a real part that is positive.
112   The latter is the well known condition for triggering instability, and explains stability criterion
113   eqn.2. In mathematical terminology, stability depends on the critical eigenvalue of the
114   community matrix that has the largest real part, i.e.,

$$\Lambda = \max_i Re(\lambda_i). \tag{3}$$

116   The system is locally stable iff $\Lambda < 0$, as in Fig.2a, since no eigenvalue has a positive real part.
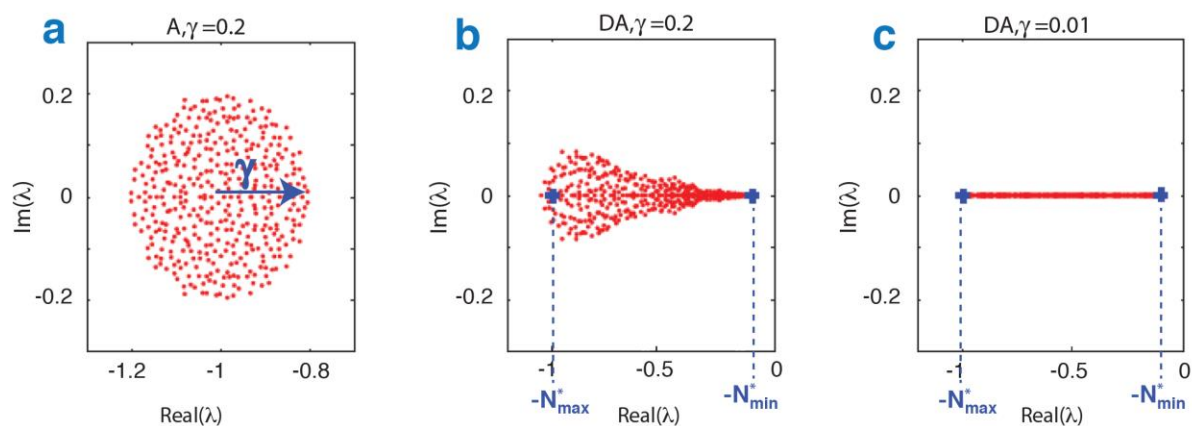
118   **Fig 2.** a) The distribution of eigenvalues of the matrix **A** in the complex plane for n=400,
119   γ=0.2. Eigenvalues are distributed according to the "circular law" and fall in a circle centred at
120   (-1,0) having radius γ (SI1). b) The eigenvalue distribution for the community matrix **S=DA**,
121   where **D**$=diag(N_i^*)$ is a positive diagonal matrix with the same matrix **A** as in (a). The circular
122   distribution disappears and is replaced by a "guitar-shaped" distribution in which the imaginary
123   components of the eigenvalues appear flattened out compared with (a). The extreme left-hand
124   and right-hand eigenvalues are predicted well by $-N_{max}^*$ and $-N_{min}^*$ (blue +). (c) Same as (b)
125   but with γ=0.01. Now nearly all eigenvalues are real and sit close to the real axis wedged
126   between $[-N_{max}^*, -N_{min}^*]$.

128   More plausible biological models that include the operation of density-dependence (DD),
129   may be framed in the form

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130
$$\frac{dN_i}{dt} = N_i\, f_i(N_1, N_2, \ldots, N_n) \qquad i=1,2,\ldots,n \qquad (4)$$

131 which provides a general characterization of many biological systems[19-21]. In these models, the
132 net per-capita growth rate of an *individual* of species-*i*, depends on its interactions with other
133 species as defined by some (often complicated) function $f_i(N_1, N_2, \ldots, N_n)$. In the simplest DD
134 model, $dN_i/dt = r\, N_i$, and each species has the same constant per-capita growth rate r, giving
135 rise to exponential growth for each species. The well known Lotka-Volterra equations are a
136 paradigmatic example of a more complex DD model, as discussed below.

137   We will be interested in determining whether or not a feasible equilibrium solution of
138 eqn.(4), $\mathbf{N}^* = (N_1^*,\ N_2^*, \ldots, N_n^*)$, is stable. But stability of this equilibrium is no longer solely
139 determined by matrices of the form $\mathbf{A}$, as defined earlier. Instead, stability is determined by the
140 critical eigenvalue of the community matrix $\mathbf{S} = \mathbf{DA}$, where the diagonal matrix $\mathbf{D}=diag(N_i^*)$
141 [2,19,20]. The matrix $\mathbf{A}$ is the usual ecological species interaction matrix, whereby a_{ij} represents the
142 *per capita* effect species-*j* has on the growth of an individual of species-*i* (see Ref.*21*). Again,
143 local stability of a feasible equilibrium is guaranteed iff the critical eigenvalue of $\mathbf{S}$ satisfies $\Lambda <$
144 0. It is important to emphasise, that even though the matrix $\mathbf{A}$ might be stable, this doesn't
145 automatically imply the matrix $\mathbf{S}=\mathbf{DA}$ is stable ($\mathbf{D}>0$), and this can potentially create problems[6-
146 10].

147   To see this in practice, a useful although hypothetical starting point is to assume that all *n*
148 population equilibria N_i^* are randomly distributed in the interval (0,1), and then examine the
149 community matrix $\mathbf{S}=\mathbf{DA}$, taking $\mathbf{A}$ as a random matrix. While $\mathbf{A}$ has eigenvalues distributed in a
150 circle in the complex plane as shown in Fig.2a, this is no longer the case for the community
151 matrix $\mathbf{S}=\mathbf{DA}$ which now has a "guitar-shaped" distribution as seen in Fig.2b. The circular law
152 for $\mathbf{A}$ becomes stretched and distorted as an outcome of the multiplication with the matrix of
153 population densities $\mathbf{D}=diag(N_i^*)$.

154   Here we show how to extract the eigenvalue distribution for $\mathbf{S}=\mathbf{DA}$. In a recent important
155 paper in the context of neuronal networks, Ahmadian et al. (2015; Ref. *22*) studied the
156 eigenvalue distribution of matrices having forms similar to the *n*x*n* stability matrix $\mathbf{S} = \mathbf{DA}.$ If
157 we set $\mathbf{A} = -\mathbf{I} + \mathbf{B}$, where $\mathbf{B}$ is a mean zero random matrix, their results imply that for large *n*,
158 the eigenvalue density of $\mathbf{S}$ is nonzero in the region of the complex plane, satisfying:

159      $$\text{trace}[(\mathbf{D}_z\, \mathbf{D}_z^\dagger)^{-1}] \geq 1/\sigma^2 \quad \text{where}\ \ \mathbf{D}_z = \mathbf{D}^{-1}(\, z\mathbf{I} - \mathbf{D})\ .$$

160 The complex variable $z = x + iy$, and trace($\mathbf{A}$)=$\sum a_{ii}$ is defined as the usual sum of the matrix
161 $\mathbf{A}$'s diagonal elements.   Applying the above inequality to the community matrix $\mathbf{S}=\mathbf{DA}$, it is not
162 hard to show that the region corresponds to those values of $z = x + iy$ for which:

163      $$T = \sum_{i=1}^{n} \frac{(N_i^*)^2}{(z+N_i^*)(\bar{z}+N_i^*)} \geq\ 1/[C\sigma^2]\ \ . \qquad (5)$$

164 The inequality specifies a well-defined region in the complex plane where the eigenvalues of $\mathbf{S}$
165 lie. The region is referred to as the "support" of the eigenvalue distribution, and unlike the RMT
166 circular law, the eigenvalue density is generally not uniform in this region.

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167   The above inequality (5) shows that the support region of the eigenvalues is determined
168   exclusively by the equilibrium populations N_i^*, σ, and connectance C. Furthermore, one
169   immediately notes that T has singularities at those points where $z = -N_i^*$, indicating that the
170   region containing the eigenvalues of **S** must necessarily envelope the population equilibria $-N_i^*$.
171   This gives an important hint of the strong relationship between the eigenvalues and the
172   population equilibria.

173   It is possible to capture the complicated eigenvalue boundary that arises by evaluating
174   eqn.5 at equality. Fig.3a plots the eigenvalue distribution for a typical community matrix **S** with
175   *n=400, σ=0.01,* and *C=1* (*i.e.*, γ =0.2), while the N_i^* are chosen from a uniform distribution
176   in the interval [0.05,1]. The boundary indicated in red is the curve deduced from eqn.5
177   evaluated at equality. Remarkably, eqn.5 accurately predicts the borders of the eigenvalue
178   distribution, and that the red border envelopes all equilibrium populations: $-N_i^* \in [-1, -0.05]$.

179   Fig.3b plots the eigenvalues of **S** for both γ =0.2 (yellow dots) and γ =0.9 (blue dots)
180   superimposed on the same graph. Note that as γ is increased to γ =0.9, the red boundary
181   expands considerably. When $\gamma > 1$, the boundary moves into the RHS of the complex plane
182   where eigenvalues have positive real parts $(Re(\lambda_i) > 0)$, and the system is unstable.

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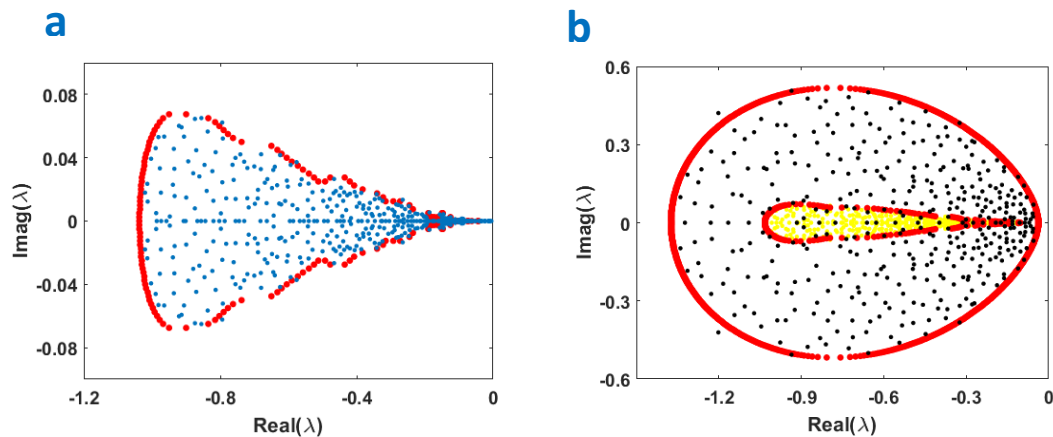
Fig 3. a) Eigenvalues (blue dots) of community matrix **S=DA** distributed in the complex plane,
where $n = 400$, γ =0.2, **D**=*diag(N_i^*)*, and N_i^* are uniformly drawn from interval [0.05,1].
Eigenvalue boundary appears as red dots, as obtained from eqn.5 evaluated at equality. b)
Similar but with eigenvalues as yellow dots for γ =0.2, and blue dots for γ =0.9. The N_i^* are
uniformly drawn from interval [0.1,1].

189   Finally, it is not hard to see from eqn.5 that if we set all $N_i^* = 1$, the May model is
190   retrieved, and all eigenvalues lie in a circle in the complex plane centred at the point $z = -1$,
191   having radius $\gamma = \sqrt{nC}\sigma$. This of course retrieves the result indicated by eqn. 2, that stability is
192   ensured if $\boldsymbol{\gamma < 1}$.

193   For a given system, the eigenvalue distribution changes as $\gamma = \sqrt{nC}\sigma$ is increased,
194   similar to that shown in Fig.3b for two different values of γ. For small γ, the eigenvalues all sit
195   in the LHS of the complex plane, and the system is stable (the critical eigenvalue is $\Lambda =$

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196    $\max_i Re(\lambda_i) < 0$). As γ is increased beyond a threshold point, the eigenvalues start to populate
197   the RHS and the system becomes unstable is ($\Lambda > 0$). For our situation, and based on eqn.5, as γ
198   is increased from zero, the threshold between stability and instability occurs when the right-most
199   point of the elliptical-like eigenvalue boundary (red line) first touches the point $z = 0$, or origin,
200   in the complex plane. That is, where $\Lambda = \max_i Re(\lambda_i) = 0$. The threshold value of γ, can be
201   found by evaluating eqn.5 at equality with $z=0$. This gives:

$$1 = \sum_{i=1}^n \frac{C(N_i^* \sigma)^2}{(0-N_i^*)(0-N_i^*)} = \sum_{i=1}^n \frac{C(N_i^* \sigma)^2}{(N_i^*)^2} = nC\sigma^2 = \gamma^2 \ .$$

203   And thus the feasible equilibrium N^* is locally stable if:

$$\gamma = \sqrt{nC}\sigma < 1, \qquad\qquad (6)$$

205   which surprisingly is independent of the positive equilibrium populations. The system is unstable
206   if $\gamma = \sqrt{nC}\sigma > 1$. We thus find that May's stability criterion is unusually general and holds for
207   DD systems having community matrices of the form **S=DA,** even though the eigenvalue
208   distributions of the latter are far from "circular."

209   Note that the identical stability criteria (2) and (6) for **A** and **S=DA** are statistical criteria,
210   and do not necessarily imply that the stability of the individual matrix **A** guarantees the stability
211   of the matrix **S=DA**. However, based on the above results, it is demonstrated in SI2 that for
212   these feasible RMT systems the matrices **A** and **S=DA** become unstable at exactly the same
213   parameter values (approximately $\gamma = 1$). That is, for a large feasible system (**D>0**),

214   stability of the interaction matrix **A** implies

215   stability of the community matrix **S=DA**.   (7)

216   where **A** is a random matrix as defined by May[1].

217

Relationship between eigenvalues of S and the equilibrium abundances: Based on an "off-
219   diagonal" matrix perturbation analysis it is possible to show that the eigenvalues λ_i of the
220   community matrix **S=DA** of RMT systems and the equilibrium abundances N_i^*, are simply
221   related, namely: $\lambda_i \simeq s_{ii} = -N_i^*$ (see Methods and SI1). The approximation holds in the range
222    $\gamma < 1$. Thus the critical eigenvalue component $\Lambda = \max_i Re(\lambda_i)$, can be well approximated by
223   the minimum equilibrium population $-N_{min}^*$:

$$\Lambda \simeq -N_{min}^* \quad . \qquad\qquad (8)$$

225   The critical eigenvalue component $\Lambda = \max_i Re(\lambda_i)$, is often used as a stability or
226   resiliency index[5,23,24]. When Λ is negative, the system is technically locally stable. However, the
227   smaller or more negative is Λ, the more resilient is the community in terms of the time taken to

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228 return to equilibrium after a small perturbation. Arnoldi et al (2017) write that this form of
229 "resilience is the most commonly used stability measure in theoretical ecology." eqn.8 implies
230 that the larger is the biomass of the rarest species (N^*_{min}), the stronger is the stability or resilience
231 of the system since it will ensure a more negative Λ, and faster return-time to equilibrium after
232 perturbation[5,24].

233 Since feasibility requires that the smallest equilibrium population N^*_{min} is
234 positive ($i.e.$, $N^*_{min}>0$), then eqn.8 makes transparent that in the regime $\gamma < 1$, feasibility is
235 linked to both local stability (which requires $\Lambda < 0$) and resilience. Note that this result does not
236 depend on any assumptions about randomness of the perturbation matrix **B**. To give an
237 indication of the performance of eqn.8 as an estimator for Λ, results for DD community matrices
238 **S**=**DA** are given in Figs.4b and SI4. Some caveats and limitations concerning this approach are
239 discussed in SI4&5.

Implications and Biological Examples

241 **Example 1. Stability and eigenvalues of Lotka-Volterra competition communities:** We now
242 proceed to explore a fully defined density-dependent biological model, rather than just an
243 abstract analysis of an arbitrary community matrix with random equilibria populations. The
244 classical Lotka-Volterra (LV) equations serve this purpose well, being one of the most successful
245 models for studying large complex systems[2-7,19]. For an n-species system, the equation for the
246 abundance of species-i is:

$$\frac{dN_i}{dt} = N_i(r_i + \sum_{j=1}^{n} a_{ij} N_j) \qquad i=1,2,\dots,n . \qquad (9)$$

248 As before, the community matrix for this system may be written as the matrix **S**=**DA**,
249 where now the populations in $\mathbf{D} = diag(N^*_i)$ are actual equilibrium solutions of model eqn.9,
250 found by setting all rates to zero. Following conventional practice, the intrinsic growth rates r_i
251 are all scaled to unity[7,10,12,14] (see SI1$)$, with positive intrinsic growth rates r_i reflecting the
252 implicit presence of resources. While some generality is lost with this scaling, it nevertheless
253 opens the door to the advantageous possibility of analytical calculations.

254 The simplest competition community is the "uniform model," where all coefficients are
255 fixed to the same constant $a_{ij} = -c,\ 0 < c < 1$, and the system is fully connected (C=1). In this
256 parameter range, the equilibrium is always feasible and stable[11]. Hence the deterministic uniform
257 model predicts that large competitive communities will satisfy two potentially advantageous
258 features of viable ecosystems, namely feasibility and stability. We will see nevertheless that
259 these seemingly stable and well-organized systems may be highly fragile in the presence of
260 environmental fluctuations.

261 In the spirit of May (1972) and Roberts (1974), a large ensemble of competitive
262 communities may be specified all of which, on the average, resemble the uniform model with
263 mean interaction strength $E(a_{ij}) = -c$. The interaction matrix **A** is given coefficients of the
264 form $a_{ij} = -[c + b_{ij}]$, where the b_{ij} are mean zero random perturbations with variance
265 Var(b_{ij})=σ^2.

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266   Stability of the competition system depends in the usual way, on the eigenvalues of the
267   community matrix **S=DA**. Fig.4a plots the eigenvalue distribution of the community matrix for a
268   typical $n=400$ species competition community ($\gamma =0.3, c=0.1$) and we see that the red boundary
269   for the support of the eigenvalues predicted by eqn.5 at equality, is an excellent fit. Note that the
270   eigenvalues in Fig.4a are all in close vicinity, and are referred to as the "bulk" eigenvalues.   The
271   support region would appear to be even more contiguous if n were increased substantially. There
272   is also an outlying real eigenvalue $\lambda= -21.41$ not shown in the figure as it is completely out of
273   scale. For competition communities, the outlying eigenvalue which would sit at the extreme left
274   of the complex plane, has no direct effect on stability. (It is in fact an outcome of having added a
275   constant term $-c$ to all interaction coefficients $a_{ij} = -\left[c + b_{ij}\right]$.)

276   Because **S** has the properties of the "Google matrix," it is shown in Refs.10&11 that for a
277   competition system, all but one of the eigenvalues of the community matrix **S=DA** are *identical*
278   (up to a scale factor of $(1 - c)$) to those for a system in which $c = 0$ (see Ref.25). But we have
279   already worked out the stability properties when $c = 0$, via eqn.6&7. Hence, as shown in [10-11],
280   it may be deduced by eqn.6 that:

281   All feasible competition systems are locally stable if $\gamma = \frac{\sqrt{n}\sigma}{1-c} < 1,$ (10)

282   apart from rare statistical exceptions.

283   In Figure 4b, the real parts of the eigenvalues of **S** are plotted against the equilibrium
284   populations $(1-c) N_i^*$ indicating $\lambda_i \simeq -(1 - c)N_i^*$, and the points sit close to the 45 degree line
285   as predicted by the theory (eqn.8).

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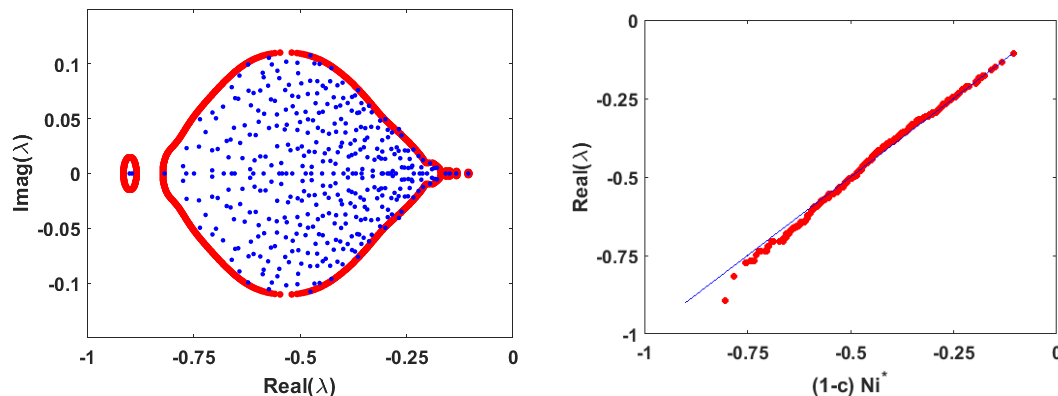
Fig 4. Competition community with $n=400, \gamma =0.3, c=0.1$. a) Boundary of the eigenvalue
distribution (red) is plotted as predicted by eqn.5 and the actual numerically calculated
eigenvalues are given (blue dots). b) The real parts of the eigenvalues of **S** are plotted against
the equilibrium populations $(1-c) N_i^*$ indicating $\lambda_i \simeq -N_i^*$, and the points sit close to the 45
degree line as predicted by eqn.8. For ease of visualisation the single outlying eigenvalue
$\lambda= -21.41$ has been removed from the plots.

9

293 **Example 2. Feasibility implies stability in the ensemble LV model** We have just seen that
294 when $\gamma < 1$ *all feasible systems* of the structure examined here are locally stable (apart from rare
295 statistical exceptions). Without having gained an understanding of the eigenvalue relationship
296 between the interaction matrix **A** and **S=DA** (see eqn.7), this result would not be available to us.
297 An important question to ask now, is whether feasible RMT systems are always locally stable?
298 This would be the case, if it could be shown that feasible systems only occur when $\gamma < 1$.

299 To address this question, we determine the parameter regime where feasible systems can
300 be found. The mathematical techniques required to accomplish this were presented in (Ref.10
301 and in Supplementary Information of Ref.11). The probability that a particular system is feasible
302 *Pr*(Feasible) requires first the determination that a typical single species has positive population
303 i.e., $p=Pr(N_i^* > 0)$.

304 **Competition communities:** Based on the equilibrium condition $\mathbf{AN^*=1}$ from eqn.9, when
305 $\gamma < 1$ a first-order approximation of the equilibrium populations of the competition equations is

$$N_i^* \approx \kappa(1 - \sum_{j=1}^n b_{ij}') \tag{11}$$

307 where κ is a positive constant and the symbol $'$ represents a division by (1-*c*). This and
308 higher order approximations, are discussed in Stone (1988, 2016-Supplementary Information).

309 [Comment: Not for publication. The following elaboration on calculating a probability of
310 feasibility is based on Stone (1988 PhD thesis) and Stone (2016 in Supplementary Information).
311 It has been added given critical readers of earlier drafts required clear direct evidence that
312 feasible systems only exist for $\gamma \ll 1$]

313 We let $X_i = 1 - \sum_{j=1}^n b_{ij}'$ and note that by the Central Limit Theorem, X_i is a normally
314 distributed random variable with mean and variance:

315 $$< X_i >= 1, \qquad Var(X_i) \approx \gamma^2 \qquad \text{where} \quad \gamma = \frac{\sqrt{n}\,\sigma}{1-c} \quad .$$

316 Thus $p=Pr(N_i^* > 0) = Pr(X_i < 1) = Pr(Z < \frac{1}{\sqrt{Var(X_i)}})$,

317 where Z is the standardized normal variate, namely $Z \sim N(0,1)$). Thus $p=Pr(N_i^* > 0)$ is purely a
318 function of the single aggregated parameter γ i.e., $p = p(\gamma)$.

319 Since the species are relatively independent, and since the *n*-species all have similar
320 characteristics, a first order estimate of system feasibility is given by the probability that *all n*-
321 species equilibria are greater than zero, namely:

$$Pr(\text{Feasible}) = p(\gamma)^n \quad . \tag{12}$$

323 Fig.1b provides a plot of the percentage of feasible competition models from a random ensemble
324 of 500 systems, as a function of disturbance γ. The graphs were generated for communities of

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325 different sizes from $n = 14$ to $n = 100$. Note carefully, that because of the exponent n in
326 eqn.12, for large communities, feasible systems are only found for

$$\gamma \ll 1. \qquad (13)$$

328 The graph shows clearly that the larger the number of species n, the more difficult it becomes to
329 generate a feasible system. Analytical predictions based on eqn.12 are shown to be accurate in
330 Fig.1b.

331 Return now to our initial query: Are all feasible systems stable? Results for competition
332 communities indicate that feasibility is very fragile and strongly dependent on the variability in
333 interaction strengths (i.e., γ) being sufficiently low; we should not expect to find feasible
334 systems unless $\gamma \ll 1$. Yet from Example 1 above, it was found that all feasible systems are
335 stable as long as $\gamma < 1$. This implies *all feasible competition systems must be stable*. It also
336 explains both in intuitive terms and theoretical terms (details in SI3) why there are no feasible-
337 stable systems when $\gamma > 1$.

338 **Mutualistic communities:** For the case of mutualist systems, the result can be generalized
339 further. Consider the LV n-species mutualistic system:

$$\frac{dN_i}{dt} = N_i(r_i + \sum_{j=1}^{n} a_{ij} N_j) \qquad i=1,2,\ldots,n. \qquad (14)$$

341 in which $a_{ij} \geq 0$, $a_{ii} = -1$, and it is assumed the matrix **A** is strongly connected (i.e.,
342 irreducible). The birth rates $r_i \geq 0$ and at least one $r_i > 0$. A simple application of M-matrix
343 theory establishes that all feasible systems are locally stable[11,26]. More recently, this result has
344 been extended and it has been shown that the mutualistic system Equations (13) possess a
345 globally asymptotically stable feasible equilibrium iff **A** is locally stable[26]. This leads to an
346 interesting situation with regards to mutualist systems, in that local stability of the interaction
347 matrix **A** and feasibility are tied in a manner that ensures that *all feasible systems are stable*.

348 Constraints on feasibility for mutualistic systems are of a similar nature to those for
349 competition (eqn.12), and demonstrate again that feasibility can only occur if $\gamma \ll 1$.

350 **Example 3. Resiliency of competition versus mutualist communities: A comparison of**
351 **methods** The "great god of competition" concept[27], has been a long-held principle amongst
352 ecologists, for which competition is viewed as the main stabilizing force in ecological
353 communities, while cooperation is viewed as essentially unstable. It is interesting to re-examine
354 this principle by studying the stability properties of the interaction matrix **A**, and comparing with
355 conclusions based on the community matrix **S=DA**.

356 **i) Community matrix S=A, indicates mutualists are destabilizing .**
357 Based on the RMT system used by *(8)* suppose the Jacobian **S** is defined as

$$s_{ij} = N_i^* a_{ij} = (m + b_{ij}) > 0, \quad s_{ii} = -1 \text{ and } m > 0, |b_{ij}| < m.$$

11

359   An underlying and unstated assumption is that all equilibrium populations are scaled to unity
360    $N_i^* = 1$, which effectively means we need only study the stability characteristics of the
361   interaction matrix **A** with $s_{ij} = a_{ij}$. Thus from the outset, the framework assumes that a feasible
362   equilibrium exists, which may be a wrong assumption.

363   The critical eigenvalue $\Lambda = \max_i Re(\lambda_i)$ of **S**=**A**, for these mutualistic systems may be
364   approximated (for large *n*) by the row sum of **S**, namely $\Lambda \cong -1 + (n-1)m$. In short, Λ
365   increases with *m*, and the feasible equilibrium becomes less and less resilient as *m* increases. A
366   sufficient condition for instability of the equilibrium is that $m > 1/(n-1)$, when the uniform
367   model loses stability.

368

369   **ii) Community matrix S=DA indicates mutualists have no effect or a positive effect on**
370   **resilience.**

371   Using the more traditional approach of directly perturbing the species-interactions, as
372   advocated here, the community matrix then has elements:

373    $$s_{ij} = N_i^* a_{ij} = N_i^* (m + b_{ij}), \quad s_{ii} = -N_i^* \text{ and } m > 0.$$

374   The equilibrium N_i^* are solutions of the the LV model (eqns.9) whereby **AN*=-1**. Thus the
375   community matrix **SN*= -1 N***, has an eigenvalue of unity.   This "outlier" eigenvalue is well
376   separated from the "bulk" as shown in Fig.5. The critical eigenvalue of **S** proves to be $\Lambda = -1$
377   for   all values *m* for which there is a feasible equilibrium.   Thus the degree of mutualistic
378   interaction *m* has *no* impact on the resiliency of a feasible equilibrium. If the average eigenvalue
379   is used as an index to gauge resiliency of a feasible equilibrium, it is possible to show that the
380   strength of mutualistic interactions *m* significantly increases the resiliency of feasible systems
381   (see eg., Ref.26 and Fig.5).

382   Note however, that feasible stable mutualistic systems exists only for $m < 1/(n-1)$,
383   i.e., only for relatively small communities having weak interactions. These communities can
384   attain high population levels ensuring the community matrix **S=DA** has negative large magnitude
385   eigenvalues (signals of strong stability). This very small parameter range for which feasibility is
386   possible, does not indicate that mutualism is a highly unstable process. Outside of the narrow
387   parameter range (i.e., for $m > 1/(n-1)$), no feasible equilibrium can even exist, so it makes no
388   sense to discuss the stability or instability characteristics of an equilibrium that does not exist.
389   The limited parameter range of coexistence, arises solely because of the difficult constraints in
390   forming a feasible system, and has little relation to equilibrium stability. The mutualist model
391   generates equilibria whose eigenvalues (real parts) become more and more negative, and thus
392   stable, as the point of infeasibility is approached.

393   Competition systems, on the other hand, are stable if

$$\sqrt{n}\sigma < 1 - c \quad,$$

12

394 according to eqn.10 and based on the community matrix **S=DA**. Hence, competition appears
395 destabilizing because increasing c, increases the critical eigenvalue $\Lambda = \max_i Re(\lambda_i) =$
396 $-(1 - c) + \sqrt{n}\sigma$, thereby decreasing resiliency.

397   The above analysis makes clear that the two different viewpoints **S=A** versus **S=DA** can
398 lead to very different conclusions about resiliency. Analysis of the eigenvalues of the interaction
399 matrix **S=A** supports classical competition theory, since it tends to show that ecological stability
400 is enhanced by competition, while mutualism is highly destabilising. However, the study of the
401 true community matrix **S=DA** (the method advocated here), finds mutualism should not be
402 viewed as a destabilising process, and can often be stabilising in terms of resiliency, while
403 competition is destabilising.

404
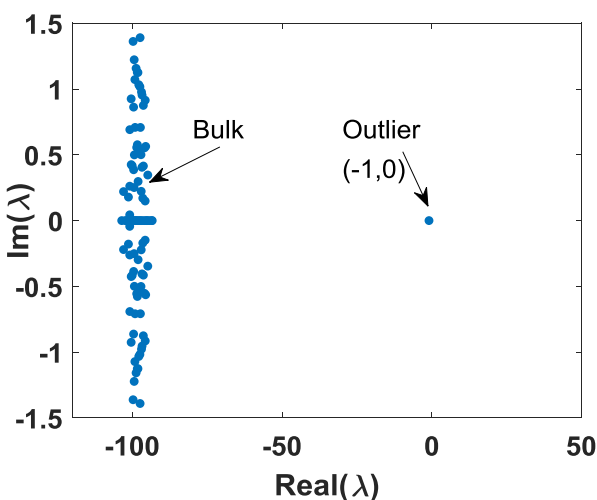
406 **Fig 5.** Eigenvalue distribution of community matrix **S=DA** for an n=100 species mutualistic
407 community (m= 0.01, $\sigma = 0.02$. The stability of **S** depends on the critical outlier eigenvalue
408 $\Lambda = -1$.

409

410 **Example 4. The impact of connectance C on feasible stable structured systems** Fig.6
411 examines the effect of connectance on predator-prey community matrices described in *(5,8)*. In
412 these communities, each pair of species can only have signs indicative of predator-prey
413 relationships of type (+,-) or (-,+), although the magnitudes of the interactions (a_{ij}) are random
414 and mean zero. Connectance C is included by incorporating a probability (1-C) that there is no
415 interaction between the species whatsoever i.e., type (0,0). Two cases are examined:

416 i) the equilibrium populations N_i^* are given random values drawn uniformly in the interval (0,1)
417 and kept fixed as connectance C is varied. Fig.6 plots both $-\Lambda$ (green) and N_{min}^* (black), and it
418 is clear that $\Lambda \simeq -N_{min}^*$, when C is varied over the full range, as predicted by eqn.8.

13

419   ii) The analysis is repeated for a Lotka-Volterra predator-prey model where the population
420   equilibria are calculated from actual model parameters ($r_i = 1$, in eqn.9). Again it is clear that
421   the relationship $\Lambda \simeq -N^*_{min}$ (red and blue respectively) holds, although now in contrast
422   N^*_{min} decreases as connectance C is increased.

423   Fig.6 clearly demonstrates that the two different models, random versus Lotka-Volterra,
424   appear to respond to changes in connectance in qualitatively different ways, yet the underlying
425   relationship $\Lambda \simeq -N^*_{min}$ is preserved, and holds for both models. Thus the effects of connectance
426   on system stability are highly model-dependent, and ultimately depends on how connectance
427   affects the smallest equilibrium population. A related analysis of the impact of connectance on
428   feasible competition systems is given in SI6.

429
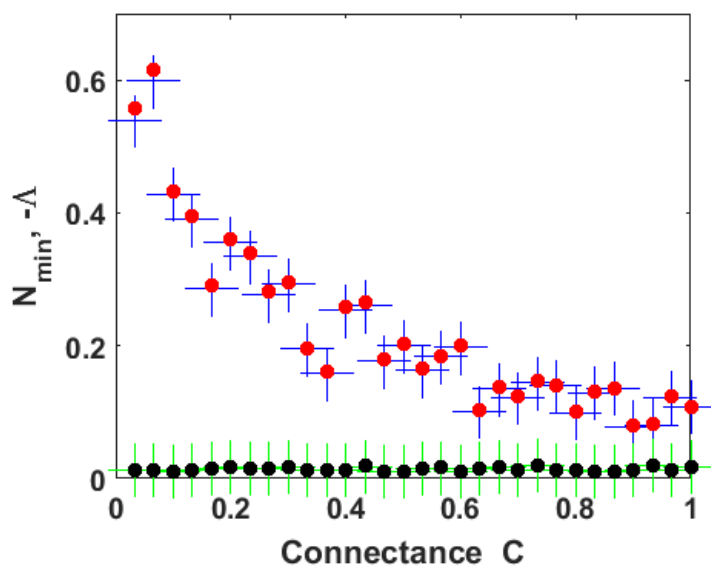
430   **Fig 6.** Predator-prey model n=200, γ =0.1. N^*_{min} (red) and $-\Lambda$ (blue) are plotted as a function of
431   connectance C, as determined from LV equations (see text). A similar analysis, but with
432   populations N^*_i randomly chosen in the interval (0,1) (N^*_{min} green +, and $-\Lambda$ black). The
433   graphs demonstrate $\Lambda \simeq -N^*_{min}$ as predicted by eqn.8.

Discussion

435   Many previous studies of biological networks have been unable to determine the stability
436   properties of the community matrix **S=DA** for large complex random matrix systems. This is
437   considered an unsolved and open problem[6,10]. Here a simple solution is presented based on the
438   trace statistics of random matrices. For feasible RMT systems, it was shown that the community
439   matrix **S=DA** transitions from stability to instability, at exactly the same parameter values for
440   which the interaction matrix **A** transitions. Thus for a large feasible system with **D**>0, stability of
441   the interaction matrix **A** implies stability of the community matrix **S=DA** (eqn.7).

442   Note that this is despite the fact that the matrix **A** has eigenvalues distributed according to
443   the circular law while the eigenvalues of the community matrix **S=DA** are distributed completely

14

444 differently (according to eqn.5). Because of the latter feature, the resilience characteristics
445 obtained from analyses of the eigenvalues of **S=DA** are different to those obtained from the
446 eigenvalues of **A**, as examples have demonstrated.

447   Feasible RMT systems were shown to be nearly always stable in the regime $\gamma<1$.
448 However, for the classical ecological RMT models examined here, feasible systems are rarely
449 found when $\gamma>1$. While these results may in some sense be model dependent, they should
450 provide a good general characterization of how the addition of heterogeneity and external
451 perturbations will affect any feasible stable system. Namely, as heterogeneity and disturbance
452 increases, the feasibility of the system will be particularly sensitive to the heterogeneity in
453 interaction, and feasibility will be lost often even before the transition from stability to instability
454 of the interaction matrix. Future research in network science may benefit from shifting focus to
455 study those factors which promote system feasibility[6,10,15].

456   Finally, if the LV systems are a good guide to real world ecological systems, they inform
457 us that large complex systems may be far more fragile than May's main result predicts. The
458 models studied here suggest that feasible stable mutualistic, competition and predator-prey
459 systems can only be found if $\gamma \ll 1$. Thus the models indicate the difficulty of assembling a
460 large complex ecosystems that is feasible, and in addition indicate their fragility to perturbation
461 in interaction strength. However, those RMT systems that can be assembled and are feasible, are
462 nearly always found to be automatically stable. This helps explain why many large ecological
463 networks *observed* in the real world (i.e., feasible systems) may be stable. It also suggests that
464 large complex systems may be even more fragile than May's main result predicts, and can be
465 completely compromised when environmental perturbations exceed relatively small threshold
466 levels. In the feasible regime, resilience of the most simple or the most complex network, is
467 entirely dependent on the smallest equilibrium abundance, and not directly determined by
468 network properties such as topology, modularity, clustering, and connectedness.
469

Methods

470

471 **1. Boundary of eigenvalue distributions:** Ahmadian et al. (2015; Ref.22) studied the
472 eigenvalue distribution of matrices having forms similar to the $n \times n$ matrix $S = M + DB$
473 (where **M** and **D** are $n \times n$ deterministic matrices and **B** a random matrix), analysed here. They
474 demonstrated[23] that for large n, the eigenvalue density of the matrix **S** is nonzero in the region of
475 the complex plane, satisfying:

476
$$trace[(M_z\, M_z^{\dagger})^{-1}] \geq 1/\sigma^2 \qquad \text{where} \ \ M_z = D^{-1}(\,zI - M\,)\,, \quad (11)$$

477 where the complex variable $z = x + iy$. This is equivalent to the region where:
478
$$trace[\ D^{-1}(\,z^*I - M)^{-1}\,(\,zI - M\,)^{-1}\,D\ ] > 1/\sigma^2\ .$$

479 Thus the eigenvalue distribution is exclusively determined by the deterministic matrix **M**, in our
480 case the equilibrium populations $\mathbf{M} = \mathbf{D} = diag(N_i^*)$, and the strength of random perturbations
481 **σ.**

15

482   Assume now that **M=DQ**, where $\mathbf{D} = diag(N_i^*)$ and **Q** is a symmetric matrix defining
483   the topology of the deterministic component of species interactions. For May's model **Q=I** is the
484   identity matrix. In the case of the competition model $\mathbf{Q} = (1-c)\mathbf{I} + c\mathbf{U}$, where all components
485   of **U** are set to $U_{ij} = 1$. To find the threshold between stability and instability for the matrix **S**,
486   we note that the eigenvalues of **M** are real, and seek the point where they change from positive to
487   negative as a parameter (eg σ or γ) is varied. We therefore seek the point where $z = 0$, and
488   evaluate eqn.5 at equality to obtain:

489
$$trace[\ \mathbf{Q}^{-2}] = 1/[C\sigma^2] \qquad . \tag{12}$$

490   • For May's system **Q=I**, and $[\mathbf{Q}^{-1}]_{ii} = 1$ $i = 1,2,...,n$ then, eqn.(12) becomes $n = 1/[C\sigma^2]$,
491   and we conclude the system is locally stable if $\gamma = \sqrt{nC}\sigma < 1$.

492   • For the case of the fully connected ($C = 1$) competition system $[\mathbf{Q}^{-1}]_{ii} = \frac{1+(n-2)c}{(1-c)(1+(n-1)c)} \cong$
493   $\frac{1}{1-c}$ for large n. We thus conclude the system is locally stable if $\gamma = \sqrt{n}\sigma/(1-c) < 1$. Here
494   it is assumed that $0 \le c < 1$.

495   • The criterion for more complex structured networks, can be determined by evaluating $[\mathbf{Q}^{-1}]_{ii}$
496   and then calculating the trace formula according to eqn.5.

497   • For the case of the fully connected mutualist systems, $a_{ij} = +m, a_{ii} = -1$, and $0 \le m <$
498   $\frac{1}{n-1}$, so that the "uniform" model is feasible. For feasible systems, the critical eigenvalue
499   $\Lambda = -1$ is an outlier from the "bulk" of the eigenvalues.

500   **2. Relation between population equilibria N_i^* and eigenvalues λ_i:** Returning to inequality
501   eqn.5, note that the left-hand-side of the expression for T has a singularity for those values of z
502   for which $z = -N_i^*$. This is visualised in Fig.7 where T is plotted as a function of z, for an
503   $n = 10$ species community with $N_1^* = 0.1$, $N_2^* = 0.2$, $N_3^* = 0.3, ..., N_{10}^* = 1$. For purposes
504   of illustration, it is assumed that z is a real number in the interval [0,1]. The function T clearly
505   explodes at all points where $z = -N_i^*$. In this cut in the complex plane, the eigenvalues are
506   predicted to be located on the x-axis (real-axis) at those points where $T > 1/[C\sigma^2]$=1000 (in
507   this example). It is clear that the eigenvalues must lie close to the population equilibria $\lambda_i \simeq$
508   $-N_i^*$. In general, the smaller the population $-N_i^*$, the more exacting is the approximation as
509   can be seen from comparing the slopes of the graphs about the equilibria (and as can be verified
510   by examining $\partial T/\partial x$).

511
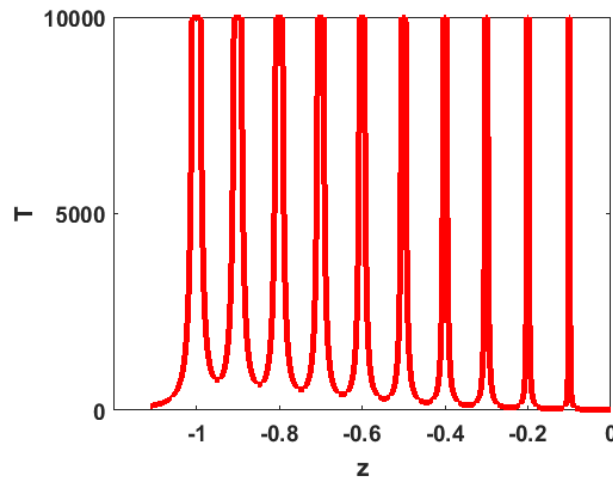
Fig 7. Plot of T in LHS of eqn.5 as a function of $x = -z$, which is real, for an $n = 10$ species community with $N_1^* = 0.1$, $N_2^* = 0.2$, $N_3^* = 0.3, ..., N_{10}^* = 1$. Singularities occur when $x = -N_i^*$.

This indicates that the smaller is σ, the closer the values of z are to the equilibrium solutions N_i^*, for which the inequality is satisfied. In fact, for σ≪ 1, we can expect $\lambda_i \simeq -N_i^*$. But this feature can already be observed in Figure 2, where it is clear that the eigenvalues in the complex plane are wedged between the vertical lines $z \simeq -N_{min}^*$ and $z \simeq -N_{max}^*$.

3. The eigenvalue approximation: $\lambda_i(S) = -N_i^* + O(\|DB\|^2)$

For the basic "neutral interaction" model, $\mathbf{A} = -\mathbf{I} + \mathbf{B}$, where $\mathbf{I}$ is the identity matrix and $\mathbf{B}$ a matrix of perturbations that are not necessarily random. In the extreme limiting case, when all off-diagonal interspecific interactions are set to zero (γ=0), then $\mathbf{A} = -\mathbf{I}$ and the community matrix is simply $\mathbf{S} = -\mathbf{D} = -diag(N_i^*)$, and the eigenvalues $\lambda_i(\mathbf{S}) = \lambda_i(\mathbf{DA}) = -N_i^*$.

When interspecific interactions are switched on (γ>0), and for reasonable assumptions (see also SI4 and [28]), the "off-diagonal" perturbation expansion is:

$$\lambda_i(\mathbf{DA}) = \lambda_i(\mathbf{D}(-\mathbf{I} + \mathbf{B})) = \lambda_i(-\mathbf{D}) + v_i^T \mathbf{DB} v_i + O(\|\mathbf{DB}\|^2).$$

Here v_i is a normalised eigenvector of $\mathbf{D}$ such that $\mathbf{D}v_i = \lambda_i(\mathbf{D})v_i$. (The spectral norm $\|\mathbf{E}\| = \sigma_{max}(\mathbf{E})$ in terms of singular values may be used.) The success of the approximation eqn.8, is because the first-order perturbation term vanishes ($v_i^T \mathbf{DB} v_i = 0$), and
$$\lambda_i(\mathbf{DA}) = \lambda_i(-\mathbf{D}) + O(\|\mathbf{DB}\|^2) \simeq -N_i^*,$$

leaving a small quadratic error term (more details are given in SI4).

The intuition behind approximation eqn.8 may be understood as follows. In the extreme limiting case, when all off-diagonal interspecific interactions are set to zero (γ=0), the eigenvalues of $\mathbf{S}=\mathbf{DA}$ have precisely the same magnitude as the equilibrium population values

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535 with $\lambda_i = -N_i^*$, and therefore eqn.8 holds exactly. Fig.2c shows a situation very near to this
536 case with γ=0.01, for which there are many weak off-diagonal interspecific interactions, and
537 nearly all of the eigenvalues sit on the real axis in close proximity to the equilibrium population
538 values $\lambda_i \simeq -N_i^*$. Denoting the smallest and largest equilibrium population as N_{min}^* and N_{max}^*
539 (in blue), then all eigenvalues should be wedged in the interval $-[N_{max}^*, N_{min}^*]$ in the complex
540 plane as seen in Fig.2c between the two demarked points in blue. But this holds to a good
541 approximation even when the intensity of the perturbed interactions is increased, as shown for
542 γ=0.2 in Fig.2b. See SI4 for more examples and a discussion of caveats regarding validity of
543 approximation.

546 **Author Contribution:** All work carried out by Lewi Stone

547 **Data Availability Statement:** No datasets were generated or analysed during the current study.

548 **Competing financial interests:** The author declares no competing financial interests.

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25. Since the community matrix **S** is a function of the competition parameter c, we will write $\mathbf{S} = \mathbf{S}(c)$. Thus, for all but the outlying spectral radius, we have the relationship $\lambda_i[\mathbf{S}(c)] = (1 - c) \, \lambda_i[\mathbf{S}(0)]$ as shown in (11).

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