Component response rate variation drives stability in large complex systems

Supplemental Information

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This supplemental information supports the manuscript "Component response rate variation drives stability in large complex systems" with all of the code required to recreate the analysis in the main text, and with additional analyses to support its conclusions. All text, code, and data underlying this manuscript are publicly available on GitHub as part of the RandomMatrixStability package.

The RandomMatrixStability package includes all functions and tools for recreating the text, this supplemental information, and running all code; additional documentation is also provided for functions as part of the package. The RandomMatrixStability package package is available on GitHub; to download it, the devtools library is needed.

```
install.packages("devtools");
library(devtools);
```

The code below installs the RandomMatrixStability package using devtools.

```
install_github("bradduthie/RandomMatrixStability");
```

While downloading this package is recommended, all relevant code is also reproduced below with explanation, so it is possible to recreate all analyses using only this supplemental information.

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38 Further explanation of γ

In a synthesis of eco-evolutionary feedbacks on community stability, Patel et al. model a system that includes a vector of potentially changing species densities (**N**) and a vector of potentially evolving traits (\mathbf{x})¹. For any species i or trait j, change in species density (N_i) or trait value (x_j) with time (t) is a function of the vectors **N** and \mathbf{x} ,

$$\frac{dN_i(t)}{dt} = N_i f_i(\mathbf{N}, \mathbf{x}),$$

$$\frac{dx_j(t)}{dt} = \epsilon g_j(\mathbf{N}, \mathbf{x}).$$

In the above, f_i and g_j are functions that define the effects of all species densities and trait values on the density of a species i and the value of trait j, respectively. Patel et al. were interested in stability when the evolution of traits was relatively slow or fast in comparison with the change in species densities¹, and this is modulated in the above by the scalar ϵ . The value of ϵ thereby determines the timescale separation between ecology and evolution, with high ϵ modelling relatively fast evolution and low ϵ modelling relative slow evolution¹.

I use the same principle that Patel et al. use to modulate the relative rate of evolution to modulate rates of component responses for S components. Following May^{2,3}, the value of a component i at time t ($v_i(t)$) is affected by the value of j ($v_j(t)$) and j's marginal effect on i (m_{ij}), and by i's response rate (γ_i),

$$\frac{dv_i(t)}{dt} = \gamma_i \sum_{j=1}^{S} m_{ij} v_j(t).$$

₅₂ In matrix notation³,

$$\frac{d\mathbf{v}(t)}{dt} = \gamma \mathbf{M}\mathbf{v}(t).$$

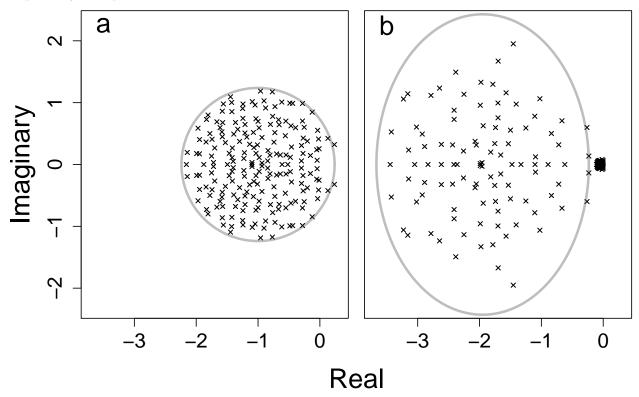
- In the above, γ is a diagonal matrix in which elements correspond to individual component response rates.
- Therefore, γM modulates the values of components and can be analysed using the techniques of May^{2,3}.

55 Code and simulations underlying Fig. 1

The sample M used for the eigenvalue distributions in Fig. 1 of the text is available on GitHub, and was produced by running the following function.

```
A0_e
               <- eigen(A0)$values;
               <- Re(A0_e);
        A0_r
        AO_i
               <- Im(A0_e);
        A1_e
               <- eigen(A1)$values;
               <- Re(A1_e);
        A1_r
        A1 i
               <- Im(A1_e);
        if(max(A0_r) >= 0 \& max(A1_r) < 0){
            return(list(A0 = A0, A1 = A1));
            break;
        print(iters);
        iters <- iters - 1;
}
```

The above find_bgamma function terminates when a matrix M is found that is not stable when all component response rates are set to $\gamma = 1$, but is stable when half of component response rates are 1.95 and half are 0.05. The function is used to illustrate the concept of how fast versus slow component responses can cause a system to become stable. Simulations were run for iter = 1000000, but terminated once an acceptable A0 and A1 were found. The code below plots the eigenvalue distributions of A0 and A1 in panels a and b, respectively. The plot itself can be recreated with the function and code below.



To find out how frequently M was stable given that all $\gamma = 1$ versus $\gamma = \{1.95, 0.05\}$, the function below was created.

```
A_dat <- rnorm(n = S * S, mean = 0, sd = 0sd);
        A_mat <- matrix(data = A_dat, nrow = S);
        C_{dat} \leftarrow rbinom(n = S * S, size = 1, prob = C);
        C_mat <- matrix(data = C_dat, nrow = S, ncol = S);</pre>
        A_mat <- A_mat * C_mat;</pre>
        gammas \leftarrow c(rep(1.95, S/2), rep(0.05, S/2))
        mu_gam <- mean(gammas);</pre>
        diag(A mat) < -1;
        Α1
                <- gammas * A_mat;
        ΑO
                <- mu_gam * A_mat;
        A0 e
                <- eigen(A0)$values;
        AO_r
                <- Re(A0_e);
        AO i
                \leftarrow Im(A0_e);
        A1_e
                <- eigen(A1)$values;
        A1_r
                \leftarrow Re(A1_e);
        A1_i
               <- Im(A1_e);
        if(max(A0_r) < 0){
             ress[iters, 1] <- 1;
             AO_count
                             <- A0_count + 1;
             }
        if(max(A1_r) < 0){
             ress[iters, 2] <- 1;</pre>
             A1 count
                             <- A1_count + 1;
        print(c(iters, A0_count, A1_count));
        iters <- iters - 1;
    return(ress);
}
```

The above functions produced the bi_pr_st data.

```
bi_pr_st <- read.csv("sim_results/bi_gamma/bi_pr_st.csv");
pr_st <- bi_pr_st[,-1];</pre>
```

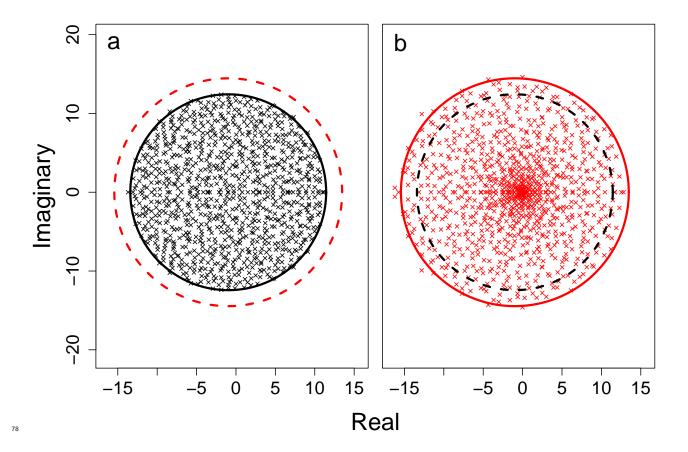
The function stab_bgamma was run for iters = 1000000, and the resulting matrix ress was returned. Each row of ress represents a single M given $\gamma = 1$ (column 1) versus $\gamma = \{1.95, 0.05\}$ (column 2). Values of 0 indicate that M was found to be unstable (at least one real component of its eigenvalues greater than or equal to zero), whereas values of 1 indicate that M was found to be stable (all real components of eigenvalues are negative). The frequencies of stable M were 1 given $\gamma = 1$ and 32 given $\gamma = \{1.95, 0.05\}$, as reported in the main text and legend of Fig. 1 (raw data are available on GitHub).

⁷⁴ Code and simulations underlying Fig. 2

Figure 2 of the main text shows eigenvalue distributions in a system where S = 1000, C = 1, and $\sigma = 0.4$. Eigenvalues can be reproduced using the code below for when $\gamma = 1$ (panel a) and $\gamma \sim \mathcal{U}(0,2)$ (panel b). The function below reproduces the figure.

```
plot_Fig_2 <- function(){
    A_comp <- NULL;
    A_dat <- rnorm(n = 1000000, mean = 0, sd = 0.4);
    A_mat <- matrix(data = A_dat, nrow = 1000);
    C_dat <- rbinom(n = 1000 * 1000, size = 1, prob = 1);</pre>
```

```
C_mat <- matrix(data = C_dat, nrow = 1000, ncol = 1000);</pre>
    A mat
              <- A_mat * C_mat;
    gammas \leftarrow runif(n = 1000, min = 0, max = 2);
    mu_gam <- mean(gammas);</pre>
    diag(A_mat) <- -1;</pre>
    A1
           <- gammas * A_mat;
    ΑO
           <- mu_gam * A_mat;
    A0 e <- eigen(A0)$values;
    A0 r \leftarrow Re(A0 e);
    A0_i \leftarrow Im(A0_e);
    A1_e <- eigen(A1)$values;
    A1_r \leftarrow Re(A1_e);
    A1_i
           <- Im(A1_e);
    AO_{vm}
                 <- AO;
    diag(A0_vm) <- NA;</pre>
    A0vec
                <- as.vector(A0_vm);</pre>
                 <- A0vec[is.na(A0vec) == FALSE];
    A0vec
    A1_vm
                 <- A1;
    diag(A1_vm) <- NA;</pre>
                 <- as.vector(A1_vm);
    A1vec
    A1vec
                 <- Alvec[is.na(Alvec) == FALSE];
    par(mfrow = c(1, 2), mar = c(0.5, 0.5, 0.5, 0.5), oma = c(5, 5, 0, 0));
    plot(AO_r, AO_i, xlim = c(-16.5, 15.5), ylim = c(-16.5, 15.5), pch = 4,
         cex = 0.7, xlab = "", ylab = "", cex.lab = 1.5, cex.axis = 1.5,
         asp = 1);
    vl \leftarrow seq(from = 0, to = 2*pi, by = 0.001);
    x0 \leftarrow sqrt(1000) * sd(A0vec) * cos(vl) + mean(diag(A0));
    y0 <- sqrt(1000) * sd(A0vec) * sin(vl);</pre>
    x1 <- sqrt(1000) * sd(A1vec) * cos(vl) + mean(diag(A1));</pre>
    y1 <- sqrt(1000) * sd(A1vec) * sin(v1);</pre>
    text(x = -15.5, y = 19, labels = "a", cex = 2);
    points(x = x0, y = y0, type = "1", lwd = 3);
    points(x = x1, y = y1, type = "1", col = "red", lwd = 3, lty = "dashed");
    plot(A1_r, A1_i, xlim = c(-16.5, 15.5), ylim = c(-16.5, 15.5), pch = 4, cex = 0.7,
         xlab = "", ylab = "", cex.lab = 1.5, cex.axis = 1.5, asp = 1, col = "red",
         yaxt = "n");
    text(x = -15.5, y = 19, labels = "b", cex = 2);
    points(x = x1, y = y1, type = "l", col = "red", lwd = 3)
    points(x = x0, y = y0, type = "1", lwd = 3, lty = "dashed");
    mtext(side = 1, "Real", outer = TRUE, line = 3, cex = 2);
    mtext(side = 2, "Imaginary", outer = TRUE, line = 2.5, cex = 2);
plot_Fig_2();
```



⁷⁹ Stability across increasing S

- ⁸⁰ Figure 3 of the main text reports the number of stable random complex systems found over 1 million iterations.
- The data used to make this figure are read into R below.

```
dat <- read.csv(file = "sim_results/C_1/random_all.csv");
dat <- dat[,-1]; # Extra row-indicating column removed</pre>
```

The table below shows the results for all simulations of random M matrices at $\sigma=0.4$ and C=1 given a range of $S=\{2,3,...,49,50\}$. In this table, the AO refers to matrices where $\gamma=1$, while A1 refers to matrices after $Var(\gamma)$ is added and $\gamma\sim\mathcal{U}(0,2)$. Each row summarises data for a given S over 1 million randomly simulated M (AO and A1). The column AO_unstable shows the number of AO matrices that are unstable, and the column AO_stable shows the number of AO matrices that are stable (these two columns sum to 1 million). Similarly, the column A1_unstable shows the number of A1 matrices that are unstable and A1_stable shows the number that are stable. The columns A1_stabilised and A1_destabilised show how many AO matrices were stabilised or destabilised, respectively, by $Var(\gamma)$.

S	$A0$ _unstable	$A0_stable$	A1_unstable	$A1_stable$	$A1_stabilised$	A1_destabilised
2	293	999707	293	999707	0	0
3	3602	996398	3609	996391	0	7
4	14937	985063	15008	984992	0	71
5	39289	960711	39783	960217	36	530
6	78845	921155	80207	919793	389	1751
7	133764	866236	136904	863096	1679	4819
8	204112	795888	208241	791759	5391	9520
9	288041	711959	291775	708225	12619	16353

\overline{S}	A0 unstable	A0 stable	A1 unstable	A1 stable	A1 stabilised	A1 destabilised
10	384024	615976	384931	615069	23153	24060
11	485975	514025	481019	518981	35681	30725
12	590453	409547	577439	422561	48302	35288
13	689643	310357	669440	330560	57194	36991
14	777496	222504	751433	248567	60959	34896
15	850159	149841	821613	178387	58567	30021
16	905057	94943	877481	122519	51255	23679
17	943192	56808	919536	80464	40854	17198
18	969018	30982	949944	50056	30102	11028
19	984301	15699	970703	29297	20065	6467
20	992601	7399	983507	16493	12587	3493
21	996765	3235	991532	8468	7030	1797
22	998693	1307	995567	4433	3884	758
23	999503	497	997941	2059	1883	321
24	999861	139	999059	941	899	97
25	999964	36	999617	383	380	33
26	999993	7	999878	122	121	6
27	999995	5	999946	54	53	4
28	1000000	0	999975	25	25	0
29	1000000	0	999997	3	3	0
30	1000000	0	999999	1	1	0
31	1000000	0	999999	1	1	0
32	1000000	0	1000000	0	0	0
33	1000000	0	1000000	0	0	0
34	1000000	0	1000000	0	0	0
35	1000000	0	1000000	0	0	0
36	1000000	0	1000000	0	0	0
37	1000000	0	1000000	0	0	0
38	1000000	0	1000000	0	0	0
39	1000000	0	1000000	0	0	0
40	1000000	0	1000000	0	0	0
41	1000000	0	1000000	0	0	0
42	1000000	0	1000000	0	0	0
43	1000000	0	1000000	0	0	0
44	1000000	0	1000000	0	0	0
45	1000000	0	1000000	0	0	0
46	1000000	0	1000000	0	0	0
47	1000000	0	1000000	0	0	0
48	1000000	0	1000000	0	0	0
49	1000000	0	1000000	0	0	0
50	1000000	0	1000000	0	0	0

Overall, the ratio of stable A1 matrices to stable A0 matrices found is greater than 1 (compare column 5 to column 3), and this ratio increases with increasing S (column 1). Hence, more randomly created complex systems (M) are generated given variation in γ than when $\gamma = 1$. The results underlying this table were produced with the rand_gen_var function below.

```
tot_res[[i-1]] <- matrix(data = 0, nrow = iter, ncol = 7);</pre>
        fea_res[[i-1]] <- matrix(data = 0, nrow = iter, ncol = 7);</pre>
        while(iter > 0){
            r vec
                      \leftarrow rnorm(n = i, mean = 0, sd = rmx);
            A0_dat
                      - rnorm(n = i * i, mean = 0, sd = 0.4);
            ΑO
                      <- matrix(data = AO_dat, nrow = i, ncol = i);
            ΑO
                      <- species_interactions(mat = A0, type = int_type);</pre>
            C dat
                      \leftarrow rbinom(n = i * i, size = 1, prob = C);
                      <- matrix(data = C_dat, nrow = i, ncol = i);
            C mat
            ΑO
                      <- A0 * C_mat;
            diag(A0) <- -1;
                      <- runif(n = i, min = 0, max = 2);
            gam1
                      <- A0 * gam1;
            Α1
            ΑO
                     <- A0 * mean(gam1);
            A0_stb <- max(Re(eigen(A0)$values)) < 0;
            A1_stb <- max(Re(eigen(A1)$values)) < 0;
            A0_fea <-\min(-1*solve(A0) %*% r_vec) > 0;
            A1_fea <-\min(-1*solve(A1) %*% r_vec) > 0;
            if(A0_stb == TRUE){
                tot_res[[i-1]][iter, 1] <- 1;
            if(A1_stb == TRUE){
                tot_res[[i-1]][iter, 2] <- 1;
            if(A0 fea == TRUE){
                fea_res[[i-1]][iter, 1] <- 1;
            if(A1_fea == TRUE){
                fea_res[[i-1]][iter, 2] <- 1;
            }
            iter
                    <- iter - 1;
        }
        print(i);
    }
    all_res <- summarise_randmat(tot_res = tot_res, fea_res = fea_res);</pre>
    return(all_res);
}
```

The above function calls the two functions species_interactions and summarise_randmat, which are provided below.

```
species_interactions <- function(mat, type = 0){
    if(type == 1){
        mat[mat > 0] <- -1*mat[mat > 0];
    }
    if(type == 2){
        mat[mat < 0] <- -1*mat[mat < 0];
    }
    if(type == 3){
        for(i in 1:dim(mat)[1]){
            for(j in 1:dim(mat)[2]){
                if(mat[i, j] * mat[j, i] > 0){
                      mat[j, i] <- -1 * mat[j, i];
                }
}</pre>
```

```
}
    }
    return(mat);
}
summarise_randmat <- function(tot_res, fea_res){</pre>
            <- length(tot res);
    all res <- matrix(data = 0, nrow = sims, ncol = 13);
    for(i in 1:sims){
        all res[i, 1]
                       <-i+1;
        # Stable and unstable
        all_res[i, 2] <- sum(tot_res[[i]][,1] == FALSE);</pre>
        all_res[i, 3] <- sum(tot_res[[i]][,1] == TRUE);
        all_res[i, 4] <- sum(tot_res[[i]][,2] == FALSE);
        all_res[i, 5] <- sum(tot_res[[i]][,2] == TRUE);
        # Stabilised and destabilised
        all_res[i, 6] <- sum(tot_res[[i]][,1] == FALSE &
                                   tot_res[[i]][,2] == TRUE);
        all_res[i, 7] <- sum(tot_res[[i]][,1] == TRUE &
                                   tot_res[[i]][,2] == FALSE);
        # Feasible and infeasible
        all_res[i, 8] <- sum(fea_res[[i]][,1] == FALSE);
        all_res[i, 9] <- sum(fea_res[[i]][,1] == TRUE);</pre>
        all_res[i, 10] <- sum(fea_res[[i]][,2] == FALSE);
        all_res[i, 11] <- sum(fea_res[[i]][,2] == TRUE);
        # Feased and defeased
        all_res[i, 12] <- sum(fea_res[[i]][,1] == FALSE &
                                   fea_res[[i]][,2] == TRUE);
        all_res[i, 13] <- sum(fea_res[[i]][,1] == TRUE &
                                   fea_res[[i]][,2] == FALSE);
    }
    cnames <- c("N", "A0_unstable", "A0_stable", "A1_unstable", "A1_stable",</pre>
                "A1_stabilised", "A1_destabilised", "A0_infeasible",
                "A0_feasible", "A1_infeasible", "A1_feasible",
                "A1_made_feasible", "A1_made_infeasible");
    colnames(all_res) <- cnames;</pre>
    return(all_res);
}
```

Note that feasibility results were ommitted for the table above, but are reported below.

Stability of ecological networks

While the foundational work of May² applies broadly to complex networks, much attention has been given specifically to ecological networks of interacting species. In these networks, the matrix M is interpreted as a community matrix and each row and column is interpreted as a single species. The effect that the density of any species i has on the population dynamics of species j is found in M_{ij} , meaning that M holds the effects of pair-wise interactions between S species⁴⁻⁶. While May's original work² considered only randomly assembled communities, recent work has specifically looked at more restricted ecological communities including competitive networks (all off-diagonal elements of M are negative), mutualist networks (all off-diagonal elements of i and i, the effect of

i on j is negative and j on i is positive, or vice versa)^{4–7}. In general, competitor and mutualist networks tend to be unstable, while predator-prey networks tend to be highly stabilising.

I investigated competitor, mutualist, and predator-prey networks following Allesina et al.⁴. To create these networks, I first generated a random matrix M, then changed the elements of M accordingly. If M was a competitive network, then the sign of any positive off-diagonal elements was reversed to be negative. If M was a mutualist network, then the sign of any positive off-diagonal elements was reversed to be positive. And if M was a predator-prey network, then all i and j pairs of elements were checked; any pairs of the same sign were changed so that one was negative and the other was positive. The species_interaction function used to do this is below.

```
species_interactions <- function(mat, type = 0){</pre>
    if(type == 1){
        mat[mat > 0] <- -1*mat[mat > 0];
    if(type == 2){
        mat[mat < 0] <- -1*mat[mat < 0];
    if(type == 3){
        for(i in 1:dim(mat)[1]){
            for(j in 1:dim(mat)[2]){
                if(mat[i, j] * mat[j, i] > 0){
                    mat[j, i] <- -1 * mat[j, i];
                }
            }
        }
    }
    return(mat);
} # Note: -1 values are added in the diagonal later
```

This function was applied to all created matrices M, then the number of stable M matrices was estimated exactly as it was in the main text for random matrices for values of S from 2 to 50 (100 in the case of the relatively more stable predator-prey interactions), except that only 100000 random M were generated instead of 1 million. This produced the data set below.

```
cdat <- read.csv(file = "sim_results/ecology/competition_C_1.csv");
mdat <- read.csv(file = "sim_results/ecology/mutualism_C_1.csv");
pdat <- read.csv(file = "sim_results/ecology/pred-prey_C_1.csv");</pre>
```

The following tables for restricted ecological communities can therefore be compared with the random M results above (but note that counts from systems with comparable probabilities of stability will be an order of magnitude lower in the tables below due to the smaller number of M matrices generated). As with the results above, in the tables below, A0 refers to matrices when $\gamma=1$ and A1 refers to matrices after $Var(\gamma)$ is added. The column A0_unstable shows the number of A0 matrices that are unstable, and the column A0_stable shows the number of A0 matrices that are stable (these two columns sum to 100000). Similarly, the column A1_unstable shows the number of A1 matrices that are unstable and A1_stable shows the number that are stable. The columns A1_stabilised and A1_destabilised show how many A0 matrices were stabilised or destabilised, respectively, by $Var(\gamma)$.

Competition

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Results for competitor interaction networks are shown below

N	${\bf A0_unstable}$	$A0_stable$	${\bf A1_unstable}$	${\bf A1_stable}$	A1_stabilised
2	48	99952	48	99952	0
3	229	99771	231	99769	0

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised
4	701	99299	704	99296	0
5	1579	98421	1587	98413	0
6	3218	96782	3253	96747	6
7	5519	94481	5619	94381	23
8	9062	90938	9237	90763	77
9	13436	86564	13729	86271	230
10	18911	81089	19303	80697	505
11	25594	74406	25961	74039	1011
12	33207	66793	33382	66618	1724
13	41160	58840	41089	58911	2655
14	50575	49425	49894	50106	3777
15	59250	40750	57892	42108	4824
16	67811	32189	65740	34260	5634
17	75483	24517	73056	26944	5943
18	82551	17449	79878	20122	5780
19	88030	11970	85204	14796	5417
20	92254	7746	89766	10234	4544
21	95233	4767	93002	6998	3695
22	97317	2683	95451	4549	2803
23	98508	1492	97122	2878	1991
24	99240	760	98407	1593	1216
25	99669	331	99082	918	739
26	99871	129	99490	510	452
27	99938	62	99732	268	240
28	99985	15	99888	112	108
29	99990	10	99951	49	46
30	100000	0	99981	19	19
31	100000	0	99993	7	7
32	100000	0	99996	4	4
33	100000	0	99998	2	2
34	100000	0	100000	0	0
			• • •		• • •
50	100000	0	100000	0	0

$_{130}$ Mutualism

 $_{\rm 131}$ $\,$ Results for mutualist interaction networks are shown below

N	${\bf A0_unstable}$	$A0_stable$	${\bf A1_unstable}$	${\bf A1_stable}$	${\bf A1_stabilised}$
2	56	99944	56	99944	0
3	3301	96699	3301	96699	0
4	34446	65554	34446	65554	0
5	86520	13480	86520	13480	0
6	99683	317	99683	317	0
7	99998	2	99998	2	0
8	100000	0	100000	0	0
9	100000	0	100000	0	0
10	100000	0	100000	0	0
11	100000	0	100000	0	0
12	100000	0	100000	0	0
50	100000	0	100000	0	0

Predator-prey
Results for predator-prey interaction networks are shown below

N	A0_	unstable	A0_	stable	A1_	_unstable	A1_	_stable	A1_	_stabilised
2		0		100000		0		100000		0
3		0		100000		0		100000		0
4		0		100000		0		100000		0
5		1		99999		1		99999		0
6		4		99996		4		99996		0
7		2		99998		2		99998		0
8		5		99995		5		99995		0
9		20		99980		21		99979		0
10		20		99980		22		99978		0
11		38		99962		39		99961		0
12		64		99936		66		99934		0
13		87		99913		91		99909		0
14		157		99843		159		99841		0
15		215		99785		227		99773		0
16		293		99707		310		99690		0
17		383		99617		408		99592		0
18		443		99557		473		99527		3
19		642		99358		675		99325		4
20		836		99164		887		99113		7
21		1006		98994		1058		98942		10
22		1153		98847		1228		98772		20
23		1501		98499		1593		98407		30
24		1841		98159		1996		98004		40
25		2146		97854		2316		97684		58
26		2643		97357		2809		97191		119
$\frac{1}{27}$		3034		96966		3258		96742		158
28		3690		96310		3928		96072		201
29		4257		95743		4532		95468		290
30		4964		95036		5221		94779		424
31		5627		94373		5978		94022		452
32		6543		93457		6891		93109		666
33		7425		92575		7777		92223		818
34		8540		91460		8841		91159		1071
35		9526		90474		9842		90158		1337
36		10617		89383		10891		89109		1624
37		12344		87656		12508		87492		2021
38		13675		86325		13877		86123		2442
39		15264		84736		15349		84651		2870
40		17026		82974		17053		82947		3363
41		18768		81232		18614		81386		3905
42		20791		79209		20470		79530		4579
43		23150		76850		22754		77246		5217
44		25449		74551		24184		75816		6285
45		27702		72298		26464		73536		6754
46		30525		69475		28966		71034		7646
47		32832		67168		31125		68875		8487
48		36152		63848		33865		66135		9479
49		38714		61286		36242		63758		10125
50		41628		58372		38508		61492		11036
						22000				

N	A0 unstable	A0 stable	A1 unstable	A1 stable	A1 stabilised
51	44483	55517	41023	58977	11704
52	48134	51866	44287	55713	12573
53	51138	48862	46721	53279	13223
54	54261	45739	49559	50441	13757
55	57647	42353	52403	47597	14324
56	60630	39370	55293	44707	14669
57	63647	36353	57787	42213	15103
58	66961	33039	60439	39561	15450
59	69968	30032	63708	36292	15246
60	72838	27162	66270	33730	15177
61	75609	24391	68873	31127	15006
62	77999	22001	71318	28682	14538
63	80616	19384	73517	26483	14510
64	83089	16911	76209	23791	13784
65	85150	14850	78086	21914	13412
66	86908	13092	80437	19563	12477
67	88671	11329	82379	17621	11718
68	90537	9463	84483	15517	10878
69	91969	8031	86233	13767	10033
70	93181	6819	87914	12086	9070
71	94330	5670	89200	10800	8401
72	95324	4676	90833	9167	7359
73	96143	3857	91805	8195	6726
74	96959	3041	93065	6935	5900
75	97543	2457	93987	6013	5222
76	97969	2031	94900	5100	4481
77	98497	1503	95756	4244	3809
78	98744	1256	96442	3558	3269
79	99045	955	96942	3058	2837
80	99276	724	97528	2472	2329
81	99481	519	97996	2004	1894
82	99556	444	98321	1679	1597
83	99691	309	98722	1278	1227
84	99752	248	98943	1057	1015
85	99833	167	99144	856	837
86	99895	105	99346	654	642
87	99925	75	99461	539	530
88	99945	55	99566	434	428
89	99976	24	99675	325	324
90	99977	23	99756	244	243
91	99982	18	99839	161	155
92	99988	12	99865	135	135
93	99994	6	99885	115	115
94	99993	7	99911	89	88
95	99998	2	99953	47	47
96	99999	1	99965	35	35
97	99999	1	99979	21	21
98	100000	0	99973	27	27
99	100000	0	99984	16	16
100	100000	0	99989	11	11

Overall, as expected⁴, predator-prey communities are relatively stable while mutualist communities are highly

unstable. But interestingly, while $Var(\gamma)$ stabilises predator-prey and competitor communities, it does not 135 stabilise mutualist communities. This is unsurprising because purely mutualist communities are characterised 136 by a very positive leading $\Re(\lambda)$, and it is highly unlikely that $Var(\gamma)$ alone will shift all real parts of 137 eigenvalues to negative values.

Different inter-connectivity (C) values

In the main text, for simplicity, I assumed inter-connectivity values of C=1, meaning that all off-diagonal 140 elements of a matrix M were potentially nonzero and sampled from a normal distribution $\mathcal{N}(0,\sigma^2)$ where $\sigma = 0.4$. Here I present four tables showing the number of stable communities given $C = \{0.3, 0.5, 0.7, 0.9\}$. 142 In all cases, uniform variation in component response time $(\gamma \sim \mathcal{U}(0,2))$ led to a higher number of stable communities than when γ did not vary ($\gamma = 1$). In contrast to the main text, 100000 rather than 1 million M were simulated. As with the results on stability with increasing S shown above, in the tables below AO refers to matrices when $\gamma = 1$, and A1 refers to matrices after $Var(\gamma)$ is added. The column A0_unstable shows the 146 number of AO matrices that are unstable, and the column AO_stable shows the number of AO matrices that are stable (these two columns sum to 100000). Similarly, the column A1 unstable shows the number of A1 148 matrices that are unstable and A1_stable shows the number that are stable. The columns A1_stabilised and A1_destabilised show how many A0 matrices were stabilised or destabilised, respectively, by $Var(\gamma)$.

All data reported below for various values of C are accessible using the below.

```
C3dat <- read.csv(file = "sim_results/C_other/rand_c-Opt3.csv");</pre>
C5dat <- read.csv(file = "sim_results/C_other/rand_c-Opt5.csv");</pre>
C7dat <- read.csv(file = "sim_results/C_other/rand_c-Opt7.csv");</pre>
C9dat <- read.csv(file = "sim_results/C_other/rand_c-Opt9.csv");</pre>
```

These objects C3dat, C5dat, C7dat, and C9dat include the results for C = 0.3, C = 0.5, C = 0.7, and C = 0.9, 152 respectively. 153

Connectance C = 0.3

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N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	5	99995	5	99995	0	0
3	6	99994	6	99994	0	0
4	24	99976	24	99976	0	0
5	59	99941	59	99941	0	0
6	98	99902	98	99902	0	0
7	160	99840	161	99839	0	1
8	290	99710	293	99707	0	3
9	430	99570	434	99566	0	4
10	648	99352	653	99347	1	6
11	946	99054	957	99043	0	11
12	1392	98608	1415	98585	4	27
13	2032	97968	2065	97935	5	38
14	2627	97373	2688	97312	10	71
15	3588	96412	3647	96353	35	94
16	5019	94981	5124	94876	51	156
17	6512	93488	6673	93327	79	240
18	8444	91556	8600	91400	165	321
19	10416	89584	10667	89333	244	495
20	13254	86746	13477	86523	425	648
21	16248	83752	16481	83519	642	875
22	19497	80503	19719	80281	929	1151
23	23654	76346	23776	76224	1368	1490

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
24	28485	71515	28389	71611	1914	1818
25	32774	67226	32483	67517	2428	2137
26	38126	61874	37411	62589	3221	2506
27	43435	56565	42418	57582	3828	2811
28	49333	50667	47840	52160	4565	3072
29	55389	44611	53381	46619	5329	3321
30	60826	39174	58388	41612	5918	3480
31	66820	33180	64043	35957	6345	3568
32	72190	27810	69036	30964	6685	3531
33	77053	22947	73587	26413	6826	3360
34	81816	18184	78157	21843	6673	3014
35	85651	14349	82041	17959	6383	2773
36	88985	11015	85657	14343	5721	2393
37	92072	7928	88805	11195	5180	1913
38	94329	5671	91444	8556	4451	1566
39	95912	4088	93295	6705	3804	1187
40	97232	2768	95201	4799	2967	936
41	98179	1821	96506	3494	2356	683
42	98826	1174	97489	2511	1786	449
43	99275	725	98312	1688	1251	288
44	99583	417	98872	1128	903	192
45	99776	224	99339	661	576	139
46	99865	135	99518	482	413	66
47	99938	62	99744	256	226	32
48	99956	44	99824	176	151	19
49	99980	20	99914	86	85	19
50	99993	7	99950	50	46	3
51	99998	2	99971	29	28	1
52	99998	2	99986	14	14	2
53	99999	1	99992	8	7	0
54	100000	0	99997	3	3	0
55	100000	0	99999	1	1	0
56	100000	0	99998	2	2	0
57	100000	0	99999	1	1	0
58	100000	0	100000	0	0	0
100	100000	0	100000	0	0	0

Connectance C = 0.5

N	A0_unstable	$A0_stable$	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	7	99993	7	99993	0	0
3	32	99968	32	99968	0	0
4	122	99878	122	99878	0	0
5	320	99680	321	99679	0	1
6	667	99333	673	99327	0	6
7	1233	98767	1252	98748	0	19
8	2123	97877	2156	97844	3	36
9	3415	96585	3471	96529	16	72
10	5349	94651	5450	94550	30	131
11	7990	92010	8185	91815	81	276

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
12	11073	88927	11301	88699	219	447
13	14971	85029	15204	84796	445	678
14	19754	80246	19992	80008	764	1002
15	25020	74980	25239	74761	1185	1404
16	30860	69140	30938	69062	1902	1980
17	37844	62156	37562	62438	2758	2476
18	44909	55091	44251	55749	3595	2937
19	52322	47678	51011	48989	4573	3262
20	60150	39850	58295	41705	5382	3527
21	67147	32853	64895	35105	5925	3673
22	74177	25823	71358	28642	6310	3491
23	80297	19703	77034	22966	6507	3244
24	85372	14628	82039	17961	6209	2876
25	89719	10281	86539	13461	5562	2382
26	92947	7053	90141	9859	4707	1901
27	95436	4564	92950	7050	3844	1358
28	97196	2804	95171	4829	2999	974
29	98300	1700	96842	3158	2115	657
30	99103	897	98033	1967	1466	396
31	99502	498	98665	1335	1068	231
32	99745	255	99185	815	696	136
33	99881	119	99572	428	375	66
34	99955	45	99788	212	191	24
35	99979	21	99900	100	95	16
36	99995	5	99950	50	50	5
37	99997	3	99970	30	28	1
38	99998	2	99986	14	13	1
39	99999	1	99991	9	9	1
40	100000	0	100000	0	0	0
41	100000	0	99999	1	1	0
42	100000	0	99999	1	1	0
43	100000	0	100000	0	0	0
	100000		100000			
50	100000	0	100000	0	0	0

Connectance C = 0.7

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	7	99993	7	99993	0	0
3	106	99894	106	99894	0	0
4	395	99605	397	99603	0	2
5	1117	98883	1123	98877	0	6
6	2346	97654	2367	97633	6	27
7	4314	95686	4388	95612	16	90
8	7327	92673	7456	92544	61	190
9	11514	88486	11792	88208	150	428
10	16247	83753	16584	83416	415	752
11	22481	77519	22759	77241	884	1162
12	29459	70541	29729	70271	1548	1818
13	37631	62369	37567	62433	2419	2355
14	46317	53683	45696	54304	3548	2927

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
15	54945	45055	53695	46305	4671	3421
16	63683	36317	61643	38357	5567	3527
17	72004	27996	69375	30625	6124	3495
18	79220	20780	76158	23842	6413	3351
19	85286	14714	82283	17717	5982	2979
20	90240	9760	87181	12819	5398	2339
21	93676	6324	91077	8923	4468	1869
22	96203	3797	94045	5955	3425	1267
23	97866	2134	96161	3839	2496	791
24	98842	1158	97633	2367	1713	504
25	99433	567	98630	1370	1079	276
26	99760	240	99259	741	655	154
27	99895	105	99576	424	377	58
28	99950	50	99790	210	194	34
29	99981	19	99915	85	80	14
30	99994	6	99952	48	47	5
31	99998	2	99972	28	28	2
32	99999	1	99992	8	8	1
33	100000	0	99997	3	3	0
34	100000	0	99999	1	1	0
35	100000	0	100000	0	0	0
	100000		100000			
50	100000	0	100000	0	0	0

Connectance C = 0.9

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	14	99986	14	99986	0	0
3	240	99760	240	99760	0	0
4	1008	98992	1016	98984	0	8
5	2708	97292	2729	97271	2	23
6	5669	94331	5755	94245	13	99
7	9848	90152	10057	89943	91	300
8	15903	84097	16201	83799	336	634
9	22707	77293	23110	76890	765	1168
10	30796	69204	31122	68878	1526	1852
11	40224	59776	40082	59918	2649	2507
12	49934	50066	49288	50712	3773	3127
13	60138	39862	58803	41197	4984	3649
14	69100	30900	67110	32890	5755	3765
15	77607	22393	74884	25116	6273	3550
16	84663	15337	81780	18220	5975	3092
17	90075	9925	87290	12710	5209	2424
18	93944	6056	91419	8581	4271	1746
19	96650	3350	94530	5470	3287	1167
20	98160	1840	96698	3302	2191	729
21	99111	889	98133	1867	1389	411
22	99588	412	98905	1095	903	220
23	99837	163	99480	520	452	95
24	99932	68	99744	256	228	40
25	99976	24	99863	137	133	20

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
26	99995	5	99950	50	49	4
27	99996	4	99986	14	13	3
28	100000	0	99993	7	7	0
29	100000	0	99996	4	4	0
30	100000	0	99998	2	2	0
31	100000	0	100000	0	0	0
50	100000	0	100000	0	0	0

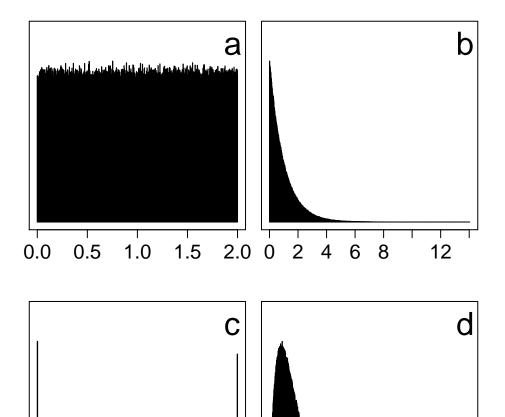
$_{ iny 18}$ Different distributions of γ

In the main text, I considered a uniform distribution of component response rates $\gamma \sim \mathcal{U}(0,2)$. The number of unstable and stable M matrices are reported in a table above across different values of S. Here I show complementary results for three different distributions including an exponential, beta, and gamma distribution of γ values. The shape of these distributions is shown in the figure below.

Distributions of component response rate (γ) values in complex systems. The stabilities of simulated complex systems with these γ distributions are compared to otherwise identical complex systems with a fixed component response rate of $\gamma=1$ across different system sizes (S; i.e., component numbers) given a unit γ standard deviation ($\sigma_{\gamma}=1$) for b-d. Distributions are as follows: (a) uniform, (b) exponential, (c) beta ($\alpha=0.5$ and $\beta=0.5$), and (d) gamma (k=2 and k=0.5). Each panel shows 1 million randomly generated k=0.50 values.



170 171



Component γ value

1.0

0.0

2.0

2

4

6

8

12

The same 100000 M matrices were used to investigate stability when applying each of these different distributions of γ values. The table below shows the number of M that were unstable (_unst) and stable (_stbl) for the exponential (Exp), beta, and gamma distributions.

fourdists <- read.csv(file = "sim_results/different_distr/four_distr_rand.csv"); kable(fourdists);

S	Exp_unst	$\rm Exp_stbl$	$beta_unst$	$beta_stbl$	gamma_unst	$gamma_stbl$
2	30	99970	30	99970	30	99970
3	355	99645	355	99645	355	99645
4	1506	98494	1512	98488	1516	98484
5	3930	96070	3971	96029	4006	95994
6	7738	92262	7844	92156	7918	92082

S	Exp_unst	Exp_stbl	beta_unst	beta_stbl	gamma_unst	$gamma_stbl$
7	13606	86394	13889	86111	13990	86010
8	20535	79465	21002	78998	21114	78886
9	28614	71386	29060	70940	29110	70890
10	38375	61625	38388	61612	38441	61559
11	48616	51384	48211	51789	47957	52043
12	59254	40746	58025	41975	57473	42527
13	68816	31184	66753	33247	66127	33873
14	77721	22279	75149	24851	74222	25778
15	84842	15158	82030	17970	81040	18960
16	90365	9635	87809	12191	86600	13400
17	94171	5829	91756	8244	90668	9332
18	96978	3022	94977	5023	94176	5824
19	98376	1624	97018	2982	96268	3732
20	99218	782	98357	1643	97765	2235
21	99678	322	99124	876	98746	1254
22	99864	136	99599	401	99323	677
23	99954	46	99783	217	99668	332
24	99978	22	99920	80	99821	179
25	99996	4	99967	33	99911	89
26	99999	1	99979	21	99960	40
27	99999	1	99990	10	99983	17
28	100000	0	99999	1	99991	9
29	100000	0	99999	1	99999	1
30	100000	0	100000	0	100000	0
31	100000	0	100000	0	99999	1
32	100000	0	100000	0	100000	0
50	100000	0	100000	0	100000	0

In comparison to the uniform distribution (a), proportionally fewer random systems are found with the exponential distribution (b), while more are found with the beta (c) and gamma (d) distributions.

177 Genetic algorithm

Ideally, to investigate the potential of $Var(\gamma)$ for increasing the proportion of stable complex systems, the search space of all possible γ vectors would be evaluated for each unique M. This is technically impossible because γ_i can take any real value between 0-2, but even rounding γ to reasonable values would result in a search space too large to practically explore. Under these conditions, genetic algorithms are highly useful tools for finding practical solutions by mimicking the process of biological evolution⁸. In this case, the practical solution is finding vectors of γ that decrease the most positive real eigenvalue of M. The genetic algorithm below achieves this by initialising a large population of 1000 different potential γ vectors and allowing this population to evolve through a process of mutation, crossover (swaping γ_i values between vectors), selection, and reproduction until either a γ vector is found where all $\Re(\lambda) < 0$ or some "giving up" critiera is met (in the below, this "giving up" critieria is met when 20 generations pass, or if the fitness increase from one generation to the next is below a certain criteria). The genetic algorithm relies on five functions. The first outer function Evo_rand_gen_var runs all of the simulations (max_sp refers to the maximum S value simulated, and iters refers to the number of M to try for each S).

```
Evo_rand_gen_var <- function(max_sp, iters, int_type = 0, rmx = 0.4, C = 1){
   tot_res <- NULL;</pre>
```

```
fea_res <- NULL;</pre>
    for(i in 2:max_sp){
                        <- i;
        nn
        A1_stt
                        <- 0;
                        <- 0;
        A2_stt
        A1_fet
                        <- 0;
        A2_fet
                        <- 0;
        iter
                        <- iters;
        tot_res[[i-1]] <- matrix(data = 0, nrow = iter, ncol = 3);</pre>
        fea_res[[i-1]] <- matrix(data = 0, nrow = iter, ncol = 2);</pre>
        while(iter > 0){
             r_vec
                      \leftarrow rnorm(n = i, mean = 0, sd = rmx);
                      <- rnorm(n = i * i, mean = 0, sd = 0.4);
             A0_dat
             ΑO
                      <- matrix(data = AO_dat, nrow = i, ncol = i);
             ΑO
                      <- species_interactions(mat = A0, type = int_type);</pre>
             C dat
                      \leftarrow rbinom(n = i * i, size = 1, prob = C);
             C_{\mathtt{mat}}
                      <- matrix(data = C_dat, nrow = i, ncol = i);
                      <- A0 * C_mat;
             diag(A0) <- -1;
                      <- runif(n = i, min = 0, max = 2);
             gam1
                      \leftarrow A0 * gam1;
             A1
             AO stb
                     <- max(Re(eigen(A0)$values)) < 0;
             A1_stb <- rand_mat_ga(A1);
             A0_fea <-\min(-1*solve(A0) \%*\% r_vec) > 0;
             A1_fea <-\min(-1*solve(A1) %*% r_vec) > 0;
             if(A0_stb == TRUE){
                 tot_res[[i-1]][iter, 1] <- 1;
             }
             if(A1_stb == TRUE){
                 tot_res[[i-1]][iter, 2] <- 1;
             if(A0_fea == TRUE){
                 fea_res[[i-1]][iter, 1] <- 1;
             if(A1 fea == TRUE){
                 fea_res[[i-1]][iter, 2] <- 1;
             }
             iter
                     <- iter - 1;
        }
        print(i);
    all_res <- summarise_randmat(tot_res = tot_res, fea_res = fea_res);</pre>
    return(all_res);
}
```

Note that Evo_rand_gen_var calls three custom sub-functions, species_interactions, rand_mat_ga, and summarise_randmat. The first simply allows for non-random interactions between components (e.g., modelling ecological interactions of random, competition, mutualism, or predator-prey).

```
species_interactions <- function(mat, type = 0){
   if(type == 1){
      mat[mat > 0] <- -1*mat[mat > 0];
   }
   if(type == 2){
```

```
mat[mat < 0] <- -1*mat[mat < 0];
}
if(type == 3){
    for(i in 1:dim(mat)[1]){
        for(j in 1:dim(mat)[2]){
            if(mat[i, j] * mat[j, i] > 0){
                mat[j, i] <- -1 * mat[j, i];
            }
        }
    }
}
return(mat);
}</pre>
```

The sub-function rand_mat_ga does the work of the genetic algorithm, searching for γ vectors that are stabilising.

```
rand_mat_ga <- function(A1, max_it = 20, converg = 0.01){</pre>
    nn
              \leftarrow dim(A1)[1];
              <- runif(n = nn*1000, min = 0, max = 1);
    rind
              <- matrix(data = rind, nrow = 1000, ncol = nn);
    inds
              <- -10;
    lastf
              <- 10;
    ccrit
    find_st <- 0;
    iter
              <- max_it;
    while(iter > 0 & find_st < 1 & ccrit > converg){
        ivar \leftarrow rep(x = 0, length = dim(inds)[1]);
        ifit \leftarrow rep(x = 0, length = dim(inds)[1]);
        isst \leftarrow rep(x = 0, length = dim(inds)[1]);
        for(i in 1:dim(inds)[1]){
             ifit[i] <- -1*max(Re(eigen(inds[i,]*A1)$values));</pre>
             ivar[i] <- var(inds[i,]);</pre>
             isst[i] <- max(Re(eigen(inds[i,]*A1)$values)) < 0;</pre>
        most_fit <- order(ifit, decreasing = TRUE)[1:20];</pre>
        parents <- inds[most_fit,];</pre>
        new_gen <- matrix(data = t(parents), nrow = 1000, ncol = nn,</pre>
                              byrow = TRUE);
                  <- rbinom(n = nn*1000, size = 1, prob = 0.2);
        \mathtt{mu\_dat}
        mu_dat2 <- rnorm(n = nn*1000, mean = 0, sd = 0.02);
        mu_dat2[mu_dat2 < 0] <- -mu_dat2[mu_dat2 < 0];</pre>
        mu_dat2[mu_dat2 > 2] <- 2;</pre>
        mu_dat3 <- mu_dat * mu_dat2;</pre>
        mu_mat <- matrix(data = mu_dat3, nrow = 1000, ncol = nn);</pre>
        new_gen <- new_gen + mu_mat;</pre>
        new_gen <- crossover(inds = new_gen, pr = 0.1);</pre>
        inds
                  <- new_gen;
        find_st <- max(isst);</pre>
        newf
                  <- mean(ifit);
                  <- newf - lastf;
        ccrit
        lastf
                  <- newf;
                  <- iter - 1;
        iter
    if(find_st == 1){
```

```
s_row <- which(isst == 1)[1];
writt <- c(nn, inds[s_row,]);
cat(writt, file = "evo_out.txt", append = TRUE);
cat("\n", file = "evo_out.txt", append = TRUE);
}
return(find_st);
}</pre>
```

The while loop in rand_mat_ga continues until either iter generations have occured, a solution γ vector is found that results in all $\Re(\lambda) < 0$, or some criteria of minimum fitness increase is observed (by default, converg = 0.01). Within the genetic algorithm, γ values are mutated, crossover occurs between γ vectors, and selection occurs in each generation such that the 20 γ vectors that produce the lowest maximum $\Re(\lambda)$ are allowed to have 50 offspring each. In mutation, any γ_i values that mutate below zero are multiplied by -1, and any values that mutate above 2 are set to 2. Note also that if a solution is found, then one such γ vector causing stability is printed to a file.

203 Crossover occurs in the crossover function below.

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After all M are simulated in Evo_rand_gen_var, the summarise_randmat formats the data into a table.

```
summarise_randmat_ga <- function(tot_res, fea_res){</pre>
            <- length(tot_res);
    all_res <- matrix(data = 0, nrow = sims, ncol = 10);
    for(i in 1:sims){
        unstables <- tot_res[[i]][,1] == FALSE & tot_res[[i]][,2] == FALSE;
                  <- tot_res[[i]][,1] == TRUE & tot_res[[i]][,2] == TRUE;
        stables
        unstabled <- tot_res[[i]][,1] == TRUE & tot_res[[i]][,2] == FALSE;
        stabled
                  <- tot_res[[i]][,1] == FALSE & tot_res[[i]][,2] == TRUE;
        non_feas <- fea_res[[i]][,1] == FALSE & fea_res[[i]][,2] == FALSE;</pre>
        feasibl
                  <- fea_res[[i]][,1] == TRUE & fea_res[[i]][,2] == TRUE;
        unfeased <- fea_res[[i]][,1] == TRUE & fea_res[[i]][,2] == FALSE;
        feased
                  <- fea_res[[i]][,1] == FALSE & fea_res[[i]][,2] == TRUE;
        foundd
                  <- tot_res[[i]][,3] == TRUE;
        all_res[i, 1] <- i + 1;
        all_res[i, 2] <- sum(unstables);</pre>
        all_res[i, 3] <- sum(stables);</pre>
        all_res[i, 4]
                      <- sum(unstabled);
        all_res[i, 5]
                      <- sum(stabled);
        all res[i, 6] <- sum(non feas);
        all_res[i, 7] <- sum(feasibl);</pre>
        all_res[i, 8] <- sum(unfeased);</pre>
```

```
all_res[i, 9] <- sum(feased);
    all_res[i, 10] <- sum(foundd);
}
return(all_res);
}</pre>
```

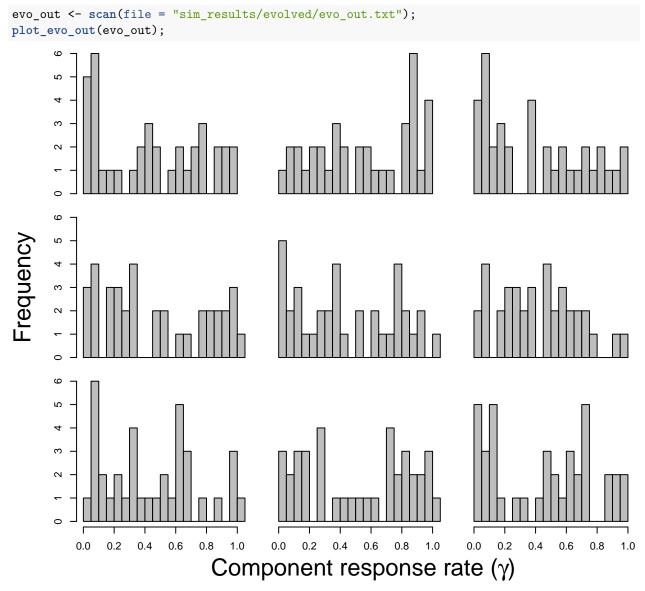
Some stability results from this table are shown below. Each histogram shows a different distribution of γ that was found to be stabilising.

A1_destabilised	A1_stabilised	A1_stable	A1_unstable	A0_stable	A0_unstable	N
0	0	9996	4	9996	4	2
0	0	9958	42	9958	42	3
0	0	9867	133	9867	133	4
0	3	9589	411	9586	414	5
0	10	9201	799	9191	809	6
0	41	8661	1339	8620	1380	7
0	147	8073	1927	7926	2074	8
0	382	7497	2503	7115	2885	9
0	684	6842	3158	6158	3842	10
1	1255	6387	3613	5133	4867	11
0	1784	5852	4148	4068	5932	12
1	2468	5530	4470	3063	6937	13
0	3060	5276	4724	2216	7784	14
0	3433	4914	5086	1481	8519	15
0	3819	4738	5262	919	9081	16
0	4063	4632	5368	569	9431	17
0	4100	4429	5571	329	9671	18
0	4037	4193	5807	156	9844	19
0	3801	3867	6133	66	9934	20
0	3545	3579	6421	34	6387	21
0	3344	3355	6645	11	6634	22
0	2947	2955	7045	8	7037	23
0	2526	2529	7471	3	7468	24
0	2184	2184	7816	0	7816	25
0	1808	1808	8192	0	8192	26
0	1320	1320	8680	0	8680	27
0	1064	1064	8936	0	8936	28
0	704	704	9296	0	9296	29
0	477	477	9523	0	9523	30
0	295	295	9705	0	9705	31
0	184	184	9816	0	9816	32
0	106	106	9894	0	9894	33
0	59	59	9941	0	9941	34
0	32	32	9968	0	9968	35
0	9	9	9991	0	9991	36
0	7	7	9993	0	9993	37
0	1	1	9999	0	9999	38
0	1	1	9999	0	9999	39
0	0	0	10000	0	10000	40

The distributions of nine γ vectors from the highest S values are shown below. Recall that 1 million random matrices were generated for the less computationally intense task of comparing M when $\gamma = 1$ versus when

 $\gamma \sim \mathcal{U}(0,2)$, so it is more informative to compare stability in column 5 above with column 3 above. This comparison shows the high number of stable M that can be produced through a targetted search of γ values, and suggests that many otherwise unstable systems could potentially be stabilised by an informed manipulation of their component response times. Such a possibility might conceivably reduce the dimensionality of problems involving stability in social-ecological or economic systems.

Distributions of γ values in vectors for the highest values of S are shown below.



The distribution of γ values found by the genetic algorithm is uniform. A uniform distribution was used to initialise γ values, so there is therefore no evidence that a particular distribution of γ is likely to be found to stabilise a matrix M.

Feasibility of complex systems

For complex systems in which individual system components (S) represent the density of some tangible quantity, it is important to consider the feasibility of the system. Feasibile equilibria assume that the values of

all system components are positive at equilibrium⁹⁻¹¹. This is of particular interest for ecological communities because population density cannot take negative values, meaning that ecological systems need to be feasible for stability to be biologically realistic¹⁰. Consequently, the use of random matrices and traditional stability critiera for making inferences in theoretical analyses of species networks has recently been criticised¹⁰. While the key results in the main text are intended to be general to all complex systems, and not restricted to species networks, I have also performed a feasibility analysis on all matrices M. This analysis reveals that feasibility is not affected by $Var(\gamma)$, meaning that for pure interacting species networks, variation in component response time (i.e., species generation time) does not affect stability at biologically realistic species densities. Nevertheless, ecological interactions do not exist in isolation in empirical systems, but instead interact with evolutionary¹, abiotic, or social-economic systems. The relevance of γ for complex system stability presented in the main text should therefore not be ignored in the broader context of ecological communities.

Dougoud et al. 10 define the following feasibility criteria for ecological systems characterised by S interacting species with varying densities.

$$x^* = -\left(\theta I + (CS)^{-\delta}A\right)^{-1}r.$$

In the above, x^* is the vector of species abundances at equilibrium (for feasibility, all values in x^* must be positive). The matrix I is the identity matrix (1s on the diagonal, 0s on the off-diagonal elements), and the value θ is strength of intraspecific competition (diagonal elements). As I have done elsewhere, diagonal values are set to -1, so $\theta = -1$. The variable C is the inter-connectivity (i.e., 'connectance') of the community, which was set to C = 1 throughout the manuscript and supplemental information, except where otherwise noted. The variable δ is a normalisation parameter that modulates the strength of interactions (σ in the main text), which are held in A. In the main text, implicitly, $\delta = 0$ underlying strong interactions. Hence, the whole $(CS)^{-\delta} = 1$, so in the above, a diagonal matrix of -1s (θI) is added to A, which has a diagonal of all zeros and an off-diagonal affecting species interactions (i.e., the expression $(CS)^{-\delta}$ relates to May's² stability criterion¹⁰ by $\frac{\sigma}{(CS)^{-\delta}}\sqrt{SC} < -1$, and hence $(CS)^{-\delta} = 1$ for the randomly simulated systems in the main text and supplemental information). The above criteria is therefore reduced to the below; note that the parenthetical in both equations produces an M matrix as used throughout the main text and supplemental information,

$$x^* = -(\theta I + A)^{-1} r.$$

To check the feasibility criteria, I therefore inverted $M = (\theta I + A)$ and multiplied elements by -1, then multiplied the resulting matrix by the vector of population growth rates r. Feasibility is satisfied if all of the elements of the resulting vector are positive.

The population growth rate for an individual species i is sampled from a normal distribution of $r_i \sim \mathcal{N}(0, 0.4^2)$, as shown in the rand_gen_var function in the section on "Stability across increasing S" above. Hence, each component i of the complex system M is assumed to be a species with a growth rate of r_i . Note that negative intrinsic growth rates are not unrealistic, and will occur in obligate mutualists in the absence of a partner.

When feasibility was evaluated with and without variation in γ , there was no increase in stability for M where γ varied as compared to where $\gamma = 1$. Results below illustrate this result, which was general to all other simulations performed.

S	A0_infeasible	A0_feasible	A1_infeasible	A1_feasible	A1_made_feasible	A1_made_infeasible
2	749978	250022	749942	250058	35552	35516
3	874519	125481	874296	125704	36803	36580
4	937192	62808	937215	62785	26440	26463
5	968776	31224	968639	31361	16319	16182
6	984313	15687	984463	15537	9006	9156
7	992149	7851	992161	7839	4991	5003

A1_made_infeasible	A1_made_feasible	A1_feasible	A1_infeasible	A0_feasible	A0_infeasible	S
2623	2644	3897	996103	3876	996124	8
1374	1361	1973	998027	1986	998014	9
707	698	960	999040	969	999031	10
345	377	486	999514	454	999546	11
188	160	208	999792	236	999764	12
87	105	135	999865	117	999883	13
47	40	55	999945	62	999938	14
24	31	36	999964	29	999971	15
11	8	9	999991	12	999988	16
3	8	9	999991	4	999996	17
3	1	1	999999	3	999997	18
2	3	3	999997	2	999998	19
0	1	1	999999	0	1000000	20
0	0	0	1000000	0	1000000	21
1	0	0	1000000	1	999999	22
0	0	0	1000000	0	1000000	23
0	0	0	1000000	0	1000000	24
0	0	0	1000000	0	1000000	25
0	0	0	1000000	0	1000000	26
0	0	0	1000000	0	1000000	27
0	0	0	1000000	0	1000000	28
0	0	0	1000000	0	1000000	29
0	0	0	1000000	0	1000000	30
0	0	0	1000000	0	1000000	31
0	0	0	1000000	0	1000000	32
0	0	0	1000000	0	1000000	33
0	0	0	1000000	0	1000000	34
0	0	0	1000000	0	1000000	35
0	0	0	1000000	0	1000000	36
0	0	0	1000000	0	1000000	37
0	0	0	1000000	0	1000000	38
0	0	0	1000000	0	1000000	39
0	0	0	1000000	0	1000000	40
0	0	0	1000000	0	1000000	41
0	0	0	1000000	0	1000000	42
0	0	0	1000000	0	1000000	43
0	0	0	1000000	0	1000000	44
0	0	0	1000000	0	1000000	45
0	0	0	1000000	0	1000000	46
0	0	0	1000000	0	1000000	47
0	0	0	1000000	0	1000000	48
0	0	0	1000000	0	1000000	49
0	0	0	1000000	0	1000000	50

Hence, in general, $Var(\gamma)$ does not appear to affect feasibility in pure species interaction networks.

261 References

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