

Reconciling complexity with stability in naturally assembling food webs

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This Material includes:

Supplementary Tables 1 and 2
Supplementary Methods
Supplementary Figures S1 to S4

Supplementary Table 1. Observed average annual biomass densities of the functional groups

Biomass (g C ha ⁻¹ cm depth ⁻¹) Developmental stage → Functional group	Schiermonnikoog				Hulshorsterzand			
	1	2	3	4	1	2	3	4
Predatory mites		5.9e-01	8.9e+00	6.5e+01			2.3e+01	2.1e+01
			1.7e+01	7.3e+01		3.0e-01	1.4e+01	2.5e+01
		2.7e+00	1.8e+01	9.2e+01			4.0e+01	2.5e+01
		3.0e-01	1.8e+01	7.4e+01		3.0e+00	1.8e+01	2.8e+01
Predatory collembolans				3.8e-01			7.5e-01	3.4e+00
				4.5e+00				6.4e+00
				3.8e-01				1.5e+01
								2.6e+00
Nematode feeding mites				1.7e+01				8.9e+00
			3.2e-01	9.3e+00				4.8e+00
				5.1e+00				7.0e+00
				1.4e+01				1.6e+01
Predatory nematodes		2.1e+01	3.0e+00	3.5e+00	5.7e+00	5.2e+01	5.5e+01	3.4e+01
	1.2e-01	4.4e+01	6.9e+00	1.9e+00	6.0e+00	4.7e+01	4.1e+01	1.6e+01
		2.3e+01	8.8e+00	1.2e+01	1.2e+01	2.2e+01	2.8e+01	6.3e+00
		1.2e+01	1.5e+01	3.3e+00	8.4e+00	2.5e+01	8.8e+01	3.1e+01
Amoebae	1.6e+01	1.6e+01	1.7e+02	4.8e+02	2.5e+00	2.2e+01	3.5e+01	2.1e+02
	6.5e+00	2.1e+01	1.0e+02	2.0e+02	9.9e+00	7.4e+01	3.1e+01	6.6e+01
	7.1e+00	4.1e+01	3.3e+02	4.5e+02	4.3e+00	2.1e+01	3.0e+01	4.5e+01
	1.3e+01	5.9e+01	2.0e+02	2.7e+02	6.5e-01	3.3e+01	2.7e+01	1.4e+02
Collembolans		2.5e+00	1.4e+01	4.8e+01		7.2e+00	6.8e+01	6.2e+01
		6.2e-01	6.3e+01	4.7e+01		7.3e+01	9.5e+01	7.5e+01
		2.8e+00	1.2e+02	6.6e+01		4.7e+01	1.9e+02	1.3e+02
		3.1e-01	2.9e+01	1.1e+02		2.4e+01	4.0e+02	1.2e+02
Cryptostigmatic mites		1.9e+01	1.1e+01	1.3e+02	5.7e-01	3.5e+01	9.5e-01	7.5e+01
	1.9e-01	1.3e+01	4.0e+01	1.6e+02	6.7e-01	2.3e+01	3.8e-01	1.2e+02
		1.2e+01	2.3e+01	1.3e+02	3.8e-01	2.0e+01	7.6e-01	1.7e+02
		7.2e+00	1.7e+01	1.1e+02		3.0e+01	1.1e+00	8.0e+01
Noncryptostigmatic mites	2.7e-01	4.9e+01	5.2e+01	6.2e+01	3.0e+00	7.9e+01	3.5e+01	2.0e+01
	3.4e-01	6.1e+01	1.1e+02	1.1e+02	2.0e+00	5.7e+01	4.6e+01	3.1e+01
	1.0e-01	4.9e+01	7.0e+01	6.0e+01	9.1e+00	5.4e+01	1.9e+01	1.6e+01
	1.4e-01	6.9e+01	6.8e+01	6.7e+01	4.3e+00	6.0e+01	2.0e+01	3.0e+01
Fungivorous nematodes	3.9e-01	4.0e+00	1.2e+01	3.9e+00	8.1e-01	9.8e-01	2.3e+01	2.7e+01
	1.0e-01	3.1e+00	1.6e+01	4.6e+00	3.1e-01	2.4e+00	2.3e+01	7.6e+00
	8.7e-02	3.2e+00	3.9e+01	9.5e+00	1.8e-01	7.0e-01	2.0e+01	1.6e+01
	9.3e-02	7.5e+00	1.1e+01	4.3e+00	1.7e-01	3.4e+00	1.6e+01	9.4e+00
Bacteriophageous mites				5.3e-01				
				2.1e-02				
				1.5e+00				2.1e-02
Bacteriophageous nematodes	1.9e-02	1.4e+01	3.5e+01	4.8e+01	4.7e-02	7.4e+00	2.5e+01	6.2e+01
	1.8e-01	5.7e+00	4.5e+01	5.6e+01	4.6e-01	2.3e+01	2.0e+01	1.1e+01
	2.0e-02	5.1e+00	4.3e+01	1.2e+02	8.2e-02	2.5e+00	1.2e+01	2.5e+01
	1.9e-02	1.3e+01	3.4e+01	6.3e+01	3.2e-02	7.0e+00	1.4e+01	3.8e+01
Flagellates	2.0e-01	3.7e+00	3.6e+01	9.7e+01	8.7e-02	1.2e+00	6.8e+00	4.7e+01
	3.7e-01	3.8e+00	3.0e+01	1.0e+02	1.3e-01	1.5e+01	7.5e+00	2.3e+01
	2.8e-01	4.0e+00	9.4e+01	1.4e+02	1.8e-01	1.0e+00	4.3e+00	4.0e+01
	2.8e-01	5.1e+00	1.5e+01	1.1e+02	1.1e-01	2.1e+00	3.8e+00	4.4e+01
Phytophageous nematodes		3.5e+00	7.2e-01			6.0e-01	2.3e+00	
	1.8e-02	2.4e+00	6.0e-02	5.6e-01		2.0e+00	1.8e+00	
		4.4e+00	9.7e-01	4.4e-01		3.2e-01	5.6e-01	1.3e-01
		2.6e+00	1.7e+00			1.4e+00	8.9e-01	
Saprophytic fungi	4.8e+01	8.7e+01	2.9e+02	3.0e+02	1.0e+01	5.2e+01	2.8e+02	1.2e+03
	3.6e+01	1.3e+02	2.4e+02	2.3e+02	1.2e+01	1.5e+01	1.7e+02	5.7e+02
	3.0e+01	1.6e+02	1.5e+02	3.4e+02	1.0e+01	1.0e+01	1.3e+02	6.9e+02
	2.1e+01	1.4e+02	1.7e+02	2.9e+02	1.5e+01	1.0e+01	1.4e+02	5.0e+02
Bacteria	1.5e+03	3.1e+03	1.7e+04	1.2e+04	1.4e+03	3.8e+03	7.3e+03	1.9e+04
	9.5e+02	4.6e+03	1.2e+04	1.3e+04	1.8e+03	5.5e+03	8.5e+03	5.0e+03
	7.9e+02	7.4e+03	2.6e+04	2.1e+04	8.3e+03	2.8e+03	7.1e+03	1.0e+04
	1.3e+03	4.3e+03	2.1e+04	2.5e+04	7.6e+02	3.3e+03	6.6e+03	3.7e+03

Observed yearly average biomass densities in the successional gradients of Schiermonnikoog (*S*) and Hulshorsterzand (*H*). In the first two stages of Hulshorsterzand we failed to detect fungi (4 cases in total). This could be attributed to the measurement equipment (note that the abundances of fungal feeders presume the presence of fungi). We therefore incorporated fungi and fungal feeders in the stability analysis of these webs, assuming a biomass value below the lowest detected value ($1.0 \times 10^1 \text{ g C ha}^{-1} \text{ cm depth}^{-1}$). The choice of the exact value did not affect the results of the analysis.

Representative food-web diagrams of the stages are shown in Figure 1 (main text). Summarising the details and exceptions to these representative webs: In stage 1 one web in *S* also contained groups 9, 10, 11 and 12, one web in *H* was without group 9. In stage 2 one web in *S* and two webs in *H* were without group 14. In stage 3 one web in *S* also contained group 16, one web in *H* also contained group 17. In stage 4 in *S* one web was without group 15 and 17, and two were without group 12, and in *H* one web was without group 12, one without group 15, and two were without groups 12 and 15.

Supplementary Table 2. Observed food-web complexity characteristics: trophic diversity, maximum chain length and link density

<i>Developmental stage →</i> <i>Complexity characteristic</i>	Schiermonnikoog				Hulshorsterzand			
	1	2	3	4	1	2	3	4
Number of trophic groups (n)	8	14	14	14	10	13	15	14
	12	13	15	16	10	14	14	14
	8	14	14	17	10	13	14	16
	8	14	14	15	9	14	14	15
Maximum food-chain length	3	5	5	6	4	4	6	6
	4	4	6	6	4	5	5	6
	3	5	5	6	4	4	5	6
	3	5	5	6	4	5	5	6
Link density (nC)	2.32	3.64	3.64	4.20	3.10	2.86	4.20	4.48
	2.88	2.86	4.20	4.48	3.10	3.64	3.64	4.48
	2.32	3.64	3.64	4.42	3.10	2.86	3.64	4.48
	2.32	3.64	3.64	4.50	3.24	3.64	3.64	4.50

Increase in complexity of the belowground food webs along the successional gradients of Schiermonnikoog and Hulshorsterzand. Both series of four successional stages (columns), each with four replicates (rows), showed a similar increase in the number of trophic groups (Spearman rank correlation, $r_s = 0.87$, $P < 0.001$), maximum food-chain length (Spearman rank correlation, $r_s = 0.90$, $P < 0.001$), and link density (Spearman rank correlation, $r_s = 0.92$, $P < 0.001$).

Supplementary Methods

Determination of intraspecific interaction in terms of death rates

Diagonal matrix elements referring to intraspecific interaction (i.e. self-damping) of the populations were modelled to depend on the mass-specific (i.e. relative to population size) non-predatory death rates in equilibrium d_j . These death rates refer to all non-predatory losses in equilibrium, including losses through intraspecific interference.

This dependence can best be explained by describing the dynamics of consumers by Lotka-Volterra type equations:

$$\frac{dX_j}{dt} = X_j \left(-b_j + \sum_{h \in \Delta_j} c_{jh} X_h - \sum_{k \in \Gamma_j} c_{jk} X_k - c_{jj} X_j \right) \quad (1)$$

where X_j is the population size of species j , b_j is the intrinsic death rate of j , c_{jh} is a coefficient of production resulting from j feeding on h , c_{jk} is a consumption coefficient, k feeding on j , Δ_j is the set of indices referring to the prey species of j , Γ_j is the set of indices referring to species that prey upon j and c_{jj} is a coefficient of intraspecific interaction. All parameters are defined positive. In equilibrium, total mass-specific non-predatory losses of a species are described by:

$$d_j = b_j + c_{jj} X_j^*. \quad (2)$$

Diagonal matrix elements, the intra-specific effects (partial derivatives near equilibrium) are $\alpha_{jj} = -c_{jj} X_j^*$.

We can define the diagonal matrix elements in terms of d_j :

$$\alpha_{jj} = -s_j d_j \quad (3)$$

where s_j is the degree (i.e. a dimensionless quantity) to which natural losses of j in equilibrium are due to intraspecific interference. It follows from equation (2) that

$0 < s_j < 1$, since $s_j = 1 - \frac{b_j}{d_j}$ and all parameters are defined positive).

Expression of stability in terms of intraspecific interaction

In our calculations we assumed for simplicity's sake that s_j is equal for all j , i.e. $s_j = s$. We expressed stability as the minimum degree of intraspecific interaction s (called diagonal strength) required for all eigenvalues to have negative real parts (see Methods).

N.B. In case we would find that matrix stability requires $s > 1$, the trophic relations documented for the webs used could not compensate for the loss rates due to mortality, consequently, these systems mathematically exceed their carrying capacity. In that case, a mathematical equilibrium in terms of Lotka-Volterra systems would require intrinsic growth rates of the species, i.e. would imply feeding from sources outside the system.

The advantage of expressing stability in terms of the diagonal lies in the fact that the eigenvalues have no direct biological interpretation, while the level of intraspecific interaction strength does have a biological, material interpretation. The terms on the diagonal representing self-damping of the organisms (dimension per time) translate to a loss rate of the organisms at steady state. Thus, this stability measure expresses both a dynamic constraint on the system (the level of self-damping needed) and an

energetic constraint: It is expressed as the loss through self-damping, relative to the total natural loss that the system can provide for, given these steady state rates, and given that the system is stable. This biological, material interpretation thus provides a basis to assess the relative importance of intraspecific competition, given a certain (interspecific) community structure. Furthermore, the use of the relative measure makes it possible to evaluate stability relative to the actual time scales of the organisms as such. Thus it separates the trivial effect of turnover times of the individual populations from the system behaviour, and enables comparing systems across time scales, in a continuous way.

Derivation of direct biomass dependencies in key loops

Stability was found to be limited by $\max_{E_3} \left\{ \left| \frac{\alpha_{23}\alpha_{12}\alpha_{31}}{d_2d_1d_3} \right|^{\frac{1}{3}} \right\}$, where E_3 is the set of

omnivorous loops of length 3, the subscripts 1, 2, and 3 refer to bottom prey, intermediate predator, and top predator in an omnivorous loop, respectively. With the

dependency of effects between predators j and prey i , $\alpha_{ij} = -\frac{F_{ij}}{B_j}$ and

$\alpha_{ji} = -e_{ij} \frac{B_j}{B_i} \alpha_{ij}$, rewriting $f_{ij} = \frac{F_{ij}}{B_j}$, this quantity can be expressed as:

$$\max_{E_3} \left\{ \left(\frac{f_{23}}{d_3} \frac{f_{12}}{d_2} e_{13} \frac{f_{13}}{d_1} \frac{B_3}{B_1} \right)^{\frac{1}{3}} \right\} \quad (1),$$

where f_{ij} is a mass-specific feeding rate of predator j on prey i in equilibrium.

Expression (1) directly depends on the top-bottom biomass ratios $\frac{B_3}{B_1}$. In case predator

feeding is directly related to prey biomass, expression (1) also depends directly on the relative contribution of a prey in a predator's diet. In the two series the omnivorous loops that had maximum weight were (in terms of the trophic groups): 8-4-2, 10-5-2, 16-10-5 and 17-10-5 (see Figure 1). In loop 10-5-2, the biomass ratio directly determining expression (1) was $\frac{B_3}{B_1}$. In the other loops (8-4-2, 16-10-5 and 17-10-5), top predators had no specific preference and only fed according to prey abundance, i.e. $p_{ij} = 1$, for $j=3$. For these loops expression (1) becomes:

$$\left(\frac{B_2 B_3}{\left(\sum_{i \in \Delta_3} B_i \right)^2} \frac{f_{12} f_3^2}{d_1 d_2 d_3} e_{13} \right)^{\frac{1}{3}} \quad (2),$$

where $f_j = \sum_{i \in \Delta_j} f_{ij}$. Thus, in these loops, the biomass ratio directly determining

expression (1) was $\frac{B_2 B_3}{\left(\sum_{i \in \Delta_3} B_i \right)^2}$.

Procedure of determining the minimum value of s for matrix stability

To assess the value of s necessary for matrix stability, a matrix was first assigned a diagonal by giving s an initial arbitrary value ($s = 1$).

If this matrix was stable (i.e. all eigenvalues had real parts) the (negative) diagonal was lowered (in absolute value, i.e. diagonal strength decreased) by a stepwise decrease of s , subtracting a proportion (0.1) of s until the matrix was no longer stable, then going back to the previous step where the matrix was stable, and refining the step

size (0.01). This procedure was repeated until a minimum step size of 0.001 (i.e. stability was determined in three decimals).

If the initial matrix was not stable, the diagonal was first raised (i.e. increased in absolute value) by increasing s an order of magnitude ($10*s$), repeating this until the matrix was stable. Then the above procedure was followed, lowering the diagonal again, until a minimal s for stability was determined in three decimals.

Supplementary Figures

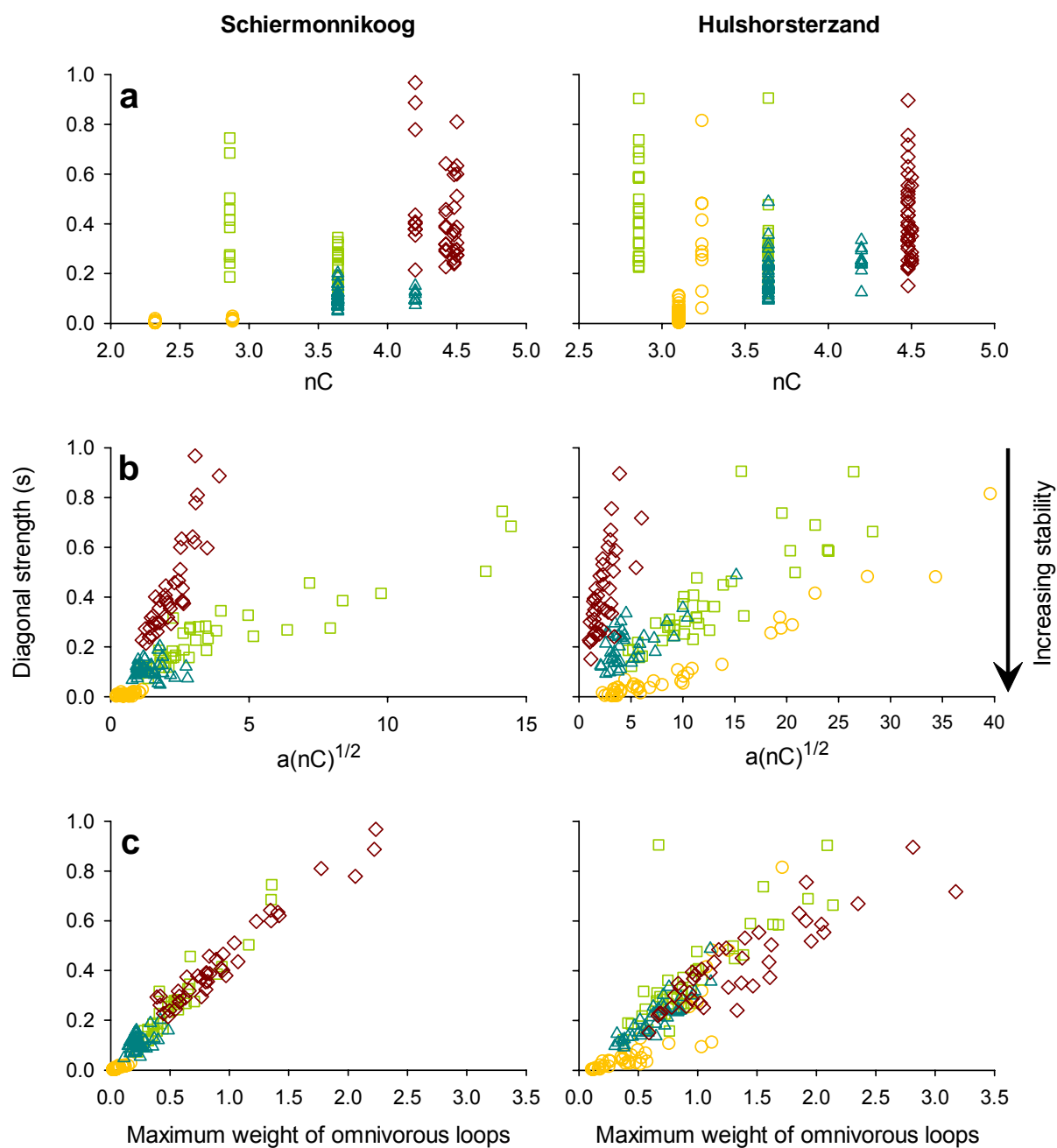
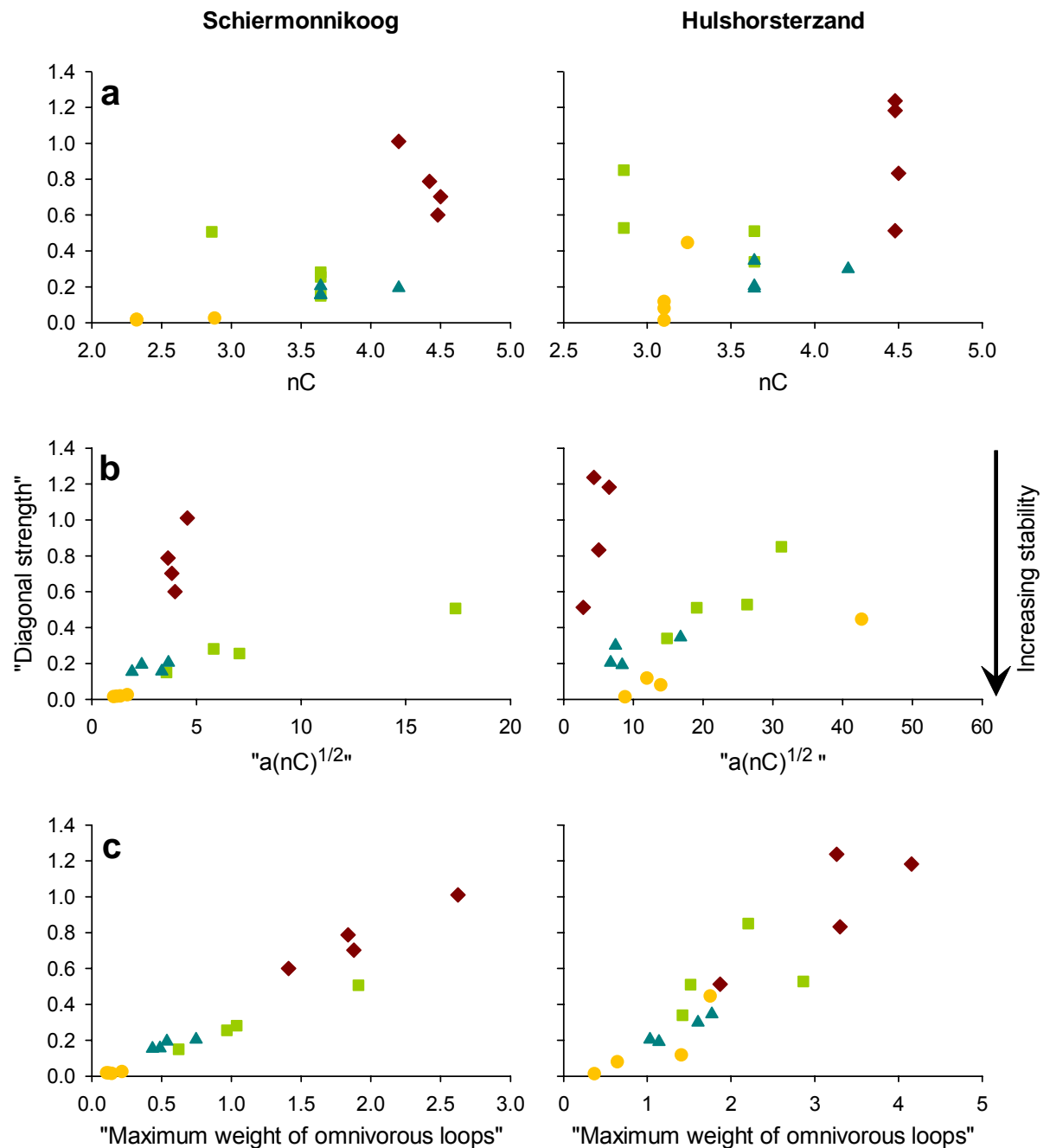


Figure S1.

Food-web stability as a result of biomass variation, related to measures of food-web structure, of S (on the left) and H (on the right). For each of the observed food webs,

10 webs were derived by sampling observed biomass densities B_i , $i=1..n$, from intervals $<1/2 B_i, 2B_i>$. **a.** Link density nC , **b.** $a(nC)^{\frac{1}{2}}$, where a is average interaction strength (see Methods), and **c.** Maximum weight of omnivorous loops. The successional stages **1** (yellow circles), **2** (green squares), **3** (blue triangles), and **4** (brown diamonds) were each represented by 4*10 food-web replications. All quantities are dimensionless, and values were based on 100 runs (see Methods).

Linear regression for **a:** $y=-0.34+0.15x$, $r^2=0.33$, $P<0.001$ (*S*) and $y=-0.08+0.10x$, $r^2=0.08$, $P<0.001$ (*H*), **b:** $y=0.09+0.053x$, $r^2=0.35$, $P<0.001$ (*S*) and $y=0.19+0.013x$, $r^2=0.18$, $P<0.001$ (*H*) and **c:** $y=0.002+0.45x$, $r^2=0.96$, $P<0.001$ (*S*) and $y=-0.005+0.33x$, $r^2=0.76$, $P<0.001$ (*H*). N (sample size) = 160 in all statistical analyses.

**Figure S2.**

This figure shows that the relation between stability and measures of food-web structure (as shown in Figure 2, main text) does not depend on the scaling of our metrics with natural death rates, nor on our specific assumption of a common s value for all organisms.

Here the stability analysis was performed without scaling, assuming equal overall intraspecific interaction for all organisms ($\alpha_{ii} = -sd_i = \alpha$). Stability was again related to measures of food-web structure, of S (on the left) and H (on the right). “Diagonal strength” corresponds to the absolute values of self-limitation of the organisms (i.e. the absolute, common, value of diagonal matrix elements of the organisms). Consequently, average interaction strengths and loop weights were also not scaled for death rates. We used the notation with inverted commas to indicate that they are not precisely the same concepts as in our main analysis, since they are not scaled. The dimension of all these three quantities is per time. Note that consequently, our assumption of a common s is released here (see Supplementary Methods). This does not have much effect on the broad patterns of stability of the observed food webs over the successional stages.

a. Link density nC **b.** “ $a(nC)^{\frac{1}{2}}$ ”, where a is the unscaled average interaction strength:

$$a = \frac{\left\{ \sum_{j \in M} \sum_{i \in \Delta_j} \alpha_{ij} \left(\sum_{j \in M} \sum_{i \in \Delta_j} \alpha_{ji} \right) \right\}^{\frac{1}{2}}}{L} \quad (\text{see Methods}), \text{ and } \mathbf{c.} \text{ “Maximum weight of}$$

omnivorous loops”, where loop weight is unscaled: “ $w^{(k)} = |\alpha_{i_1 i_2} \alpha_{i_2 i_3} \dots \alpha_{i_k i_1}|^{1/k}$ ” (see Methods). The successional stages **1** (yellow circles), **2** (green squares), **3** (blue triangles), and **4** (brown diamonds) were each represented by 4 food-web replications. Values were based on 100 runs (see Methods).

Linear regression for **a:** $y = -0.68 + 0.28x$, $r^2 = 0.50$, $P = 0.002$ (S) and $y = -0.74 + 0.33x$, $r^2 = 0.29$, $P = 0.031$ (H), **b:** $y = 0.20 + 0.03x$, $r^2 = 0.12$, $P = 0.180$ (S) and $y = -0.50 - 0.001x$,

$r^2 = -0.002$, $P = 0.885$ (H) and **c**: $y = -0.05 + 0.39x$, $r^2 = 0.94$, $P < 0.001$ (S) and $y = -0.14 + 0.33x$, $r^2 = 0.84$, $P < 0.001$ (H).). $N = 16$ in all statistical analyses.

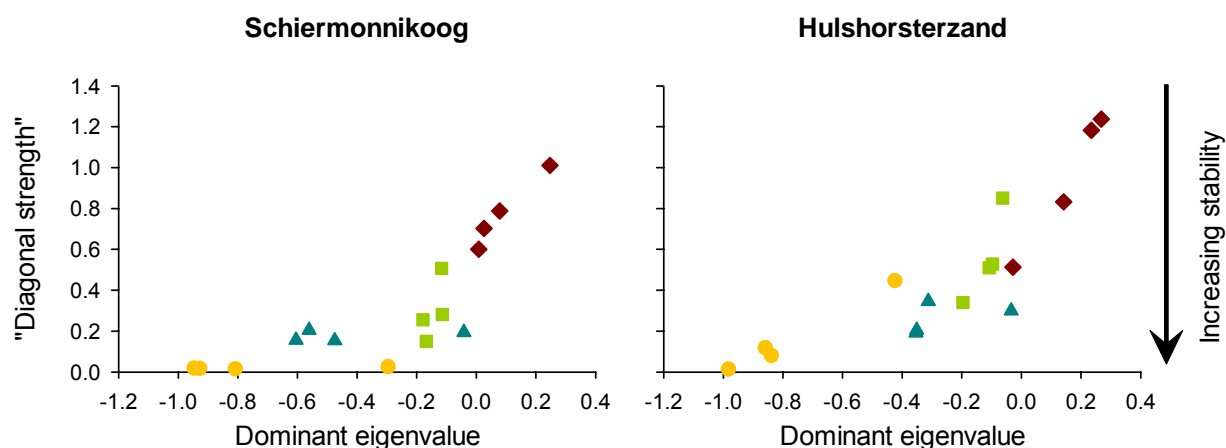


Figure S3.

This figure shows that our measure of the minimal diagonal needed for matrix stability corresponds closely with the dominant eigenvalue of matrices with a fixed diagonal. “Diagonal strength” measures food-web stability as in Fig. S2 with equal intraspecific interaction for all organisms. It is related to maximum eigenvalues of the food webs with the intraspecific interactions of the organisms all fixed at -1 (i.e. $\alpha_{ii} = -sd_i = -1$, for all organisms). The results again for *S* (on the left) and *H* (on the right). Successional stages **1** (yellow circles), **2** (green squares), **3** (blue triangles), and **4** (brown diamonds), were each represented by 4 food-web replications. All quantities have the dimension per time, and values are mean values based on 100 runs (see Methods).

Correlation coefficients: $r^2=0.80$, $N=16$, $P<0.001$ (*S*) and $r^2=0.85$, $P<0.001$ (*H*).

N.B. There is no principal difference between expressing stability in terms of the dominant eigenvalue and expressing stability in terms of the diagonal. The advantage of using *s* as a stability measure, instead of using the dominant eigenvalue, given a fixed diagonal, is that it provides a biological, material interpretation of stability, and

also allows us to assess stability relative to the intrinsic time scales of the organisms as such, i.e. compare systems of any type, across all time scales (see explanation in Supplementary Methods).

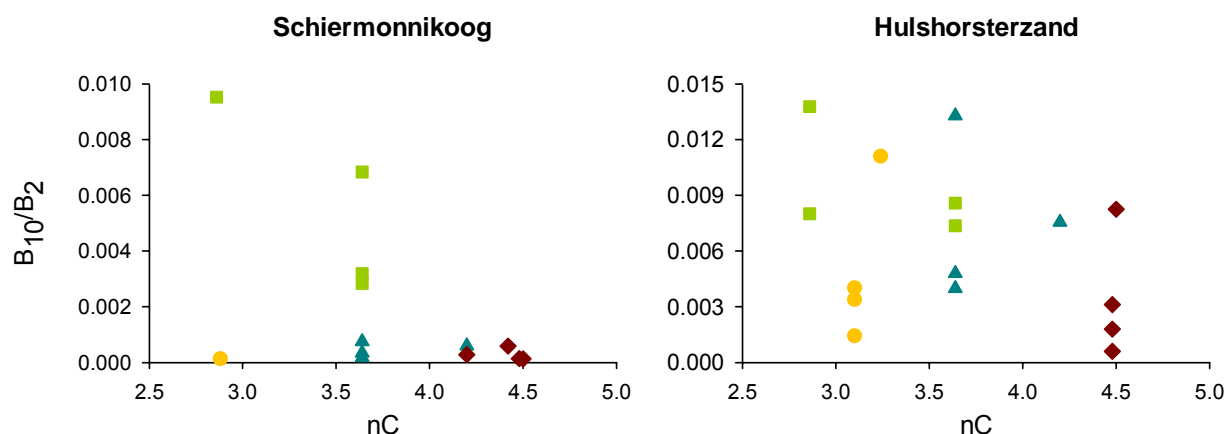


Figure S4. Complexity (Link density nC) related to the predator-prey biomass ratio between predatory nematodes and bacteria, in S (on the left) and H (on the right). Successional stages 1 (yellow circles), 2 (green squares), 3 (blue triangles), and 4 (brown diamonds), are all represented by 4 food webs, apart from the first stage in S , where in three webs predatory nematodes were not present.

The figure shows a pattern over time, in both gradients: This biomass ratio increased from the first to the second stage, when predatory nematodes were the top predators ($P < 0.05$ (H)) and decreased again with complexity in the later stages (stages 2-4) when predatory nematodes were no longer the top predators. Spearman rank correlation for the decrease over successional stages 2 to 4: $r_s = -0.86$, $N=12$, $P < 0.001$ (S) and $r_s = -0.62$, $N=12$, $P = 0.031$ (H). Linear regression for the decrease with nC over the stages 2 to 4: $y=0.02-0.005x$, $r^2=0.55$, $N=12$, $P=0.006$ (S) and $y=0.02-0.004x$, $r^2=0.40$, $N=12$, $P=0.027$ (H). [AMN: I hope you allow me to correct this small but nasty error in the number of data points in the statistical analysis, N . (N was only added in our last editing round, and by mistake the number of points in the graph were given - the number of data points of the analysis is not the same as in the graph,

and only refers to the three last stages, as indicated in the text line 9 and 10).

Uncorrected, this error would cause confusion.]