

A. Online Appendix

A.1. Detailed description of food web attributes

The *trophic fractions* are as defined in Cohen (1989b). The trophic fractions are the fractions of species that are basal (i.e. had no prey), intermediate, and top (had no predators), denoted B, I, and T, respectively. These measures are summarised using a multinomial regression, found by the maximum likelihood method, as described in Murtaugh & Kollath (1997) and Murtaugh (1994). In all cases, the significance testing is corrected with the dispersion parameter (Murtaugh & Kollath 1997).

The *mean maximum similarity* is as defined in Williams & Martinez (2000, p. 181): “Trophic similarity of a pair of species ($s_{i,j}$) is the number of predators and prey shared in common divided by the pair’s total number of predators and prey”. The mean maximum similarity, s_{\max} , is then found by taking the average of all species’ largest similarity index.

The *trophic level*, TL, is as defined in Williams & Martinez (2004). Because Williams & Martinez (2004) observed that short-weighted trophic level provided the best estimate of true flow-based trophic level for binary webs, this study will only present results for that measure. The short-weighted trophic level is the average of the shortest-path trophic level and the prey-averaged trophic level. The shortest-path trophic level is 1 + the shortest chain length from the species to a basal species, and prey-averaged trophic level is the mean trophic level of all of the species’ trophic resources. The method of Levine (1980) is used to find the prey-averaged trophic level. From this the mean trophic level, $\bar{\text{TL}}$, and maximum trophic level or trophic height, TL_{\max} , can be found.

The *degree of omnivory* is measured as the standard deviation of a species’ preys’ trophic levels (Williams & Martinez 2000).

The *generality*, G , and *vulnerability*, V , is as defined in Schoener (1989). Generality is

the average number of prey eaten per predator, and vulnerability is the average number of predators per prey.

The *standard deviation of generality and vulnerability*, $SD(G)$ and $SD(V)$, is as defined in Williams & Martinez (2000). The reader should note that the definition of ‘generality’ and ‘vulnerability’ used by Williams & Martinez (2000) to find the standard deviation differs from the original definition in Schoener (1989), in that Williams & Martinez (2000) calculated these measures for all species, whether they are prey, predator, or both. This is not made explicitly clear, but can be deduced from their comment “[n]ormalising with L/S makes s.d. comparable across different webs by forcing mean G_i and V_i to equal 1” (p. 180). From Williams & Martinez (2000), if $\hat{a}_{i,j} = 1$ when species j consumes species i , and 0 if not, then generality is $G_i = \frac{1}{L/n} \sum_{j=1}^n \hat{a}_{i,j}$ and vulnerability is $V_i = \frac{1}{L/n} \sum_{j=1}^n \hat{a}_{j,i}$.

A *motif or anti-motif* is as defined in Milo et al. (2002), which is a pattern of interconnections that occurs in a network at frequencies significantly higher than random equivalent networks. All possible motifs of size 3, 4 and 5 are shown in Figures A1, A2, and A3, respectively. ‘Algorithm B’ from Milo et al. (2002) was used to create the randomised equivalent graphs with which Z-scores were calculated. In this study, a motif or an anti-motif is defined as any motif that has a Z-score greater than $|2|$ when compared to randomised versions of that web. The motifs identified as common in empirical webs by Milo et al. (2002) were the ‘three-chain’ and ‘bi-parallel’, denoted 3-motif 2 and 4-motif 15, respectively.

A.2. Motifs in algorithm webs

Table A1. Percentage of food webs in each class with a motif or anti-motif. The two motifs identified in Milo et al. (2002) as common in real food webs, the ‘three-chain’, and ‘bi-parallel’, are indicated.

| Name | n | L | Control | | | | Impermanent | | | | Permanent | | | |
|-----------------------------|-----|-----|---------|---|----|----|-------------|---|----|----|-----------|----|----|----|
| | | | NC | | TC | | NC | | TC | | NC | | TC | |
| | | | – | + | – | + | – | + | – | + | – | + | – | + |
| Any 3-motif | 3 | ... | 14 | | 61 | | 0 | | 50 | | 10 | | 30 | |
| 3-motif ID (three-chain) | 1 | 3 | 2 | 5 | 5 | 1 | 50 | | | 50 | 10 | | 4 | 26 |
| | 2 | 3 | 2 | | | | 61 | | | 50 | 5 | | | 22 |
| | 3 | 3 | 2 | 5 | 5 | 1 | 50 | | | 50 | 10 | | 4 | 26 |
| | 4 | 3 | 3 | 5 | 5 | 50 | 1 | | 50 | | 10 | 26 | 4 | |
| | 5 | 3 | 3 | | 5 | 11 | | | | | 5 | | | |
| Any 4-motif | 4 | ... | 62 | | 97 | | 70 | | 88 | | 52 | | 96 | |
| 4-motif ID | 1 | 4 | 2 | 5 | 5 | 1 | 40 | | | 25 | | | | 22 |
| | 2 | 4 | 2 | | | 8 | 13 | 5 | | 13 | | | 9 | 13 |
| | 3 | 4 | 2 | | | 25 | 1 | | 13 | | 5 | | 4 | |
| | 4 | 4 | 2 | | | | 42 | | | 25 | 5 | | 4 | 9 |
| | 5 | 4 | 2 | | 5 | | 70 | | | 63 | 5 | | | 26 |
| | 6 | 4 | 2 | | 10 | 2 | 65 | | | 38 | 5 | | | 48 |
| | 7 | 4 | 2 | | | 25 | 2 | | 25 | | 10 | | 39 | |
| | 8 | 4 | 2 | | | | 42 | | | 50 | 5 | 5 | | 17 |
| | 9 | 4 | 3 | 5 | 10 | 21 | 1 | | 5 | 13 | | | | 4 |
| | 10 | 4 | 3 | | 10 | 11 | 2 | 5 | | | | 19 | | 4 |
| | 11 | 4 | 3 | | 5 | 8 | 6 | | 9 | 13 | | 10 | | 4 |
| | 12 | 4 | 3 | | 5 | 5 | 3 | | | 25 | | 10 | | 9 |

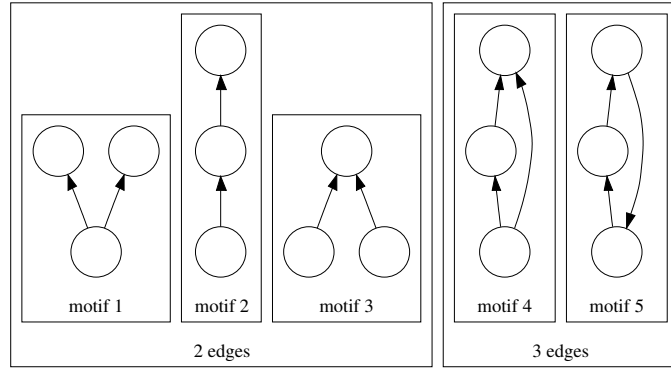


Fig. A1.— Diagrams of the 3-motifs. Circles are species and edges represent the flow of energy from one species to another.

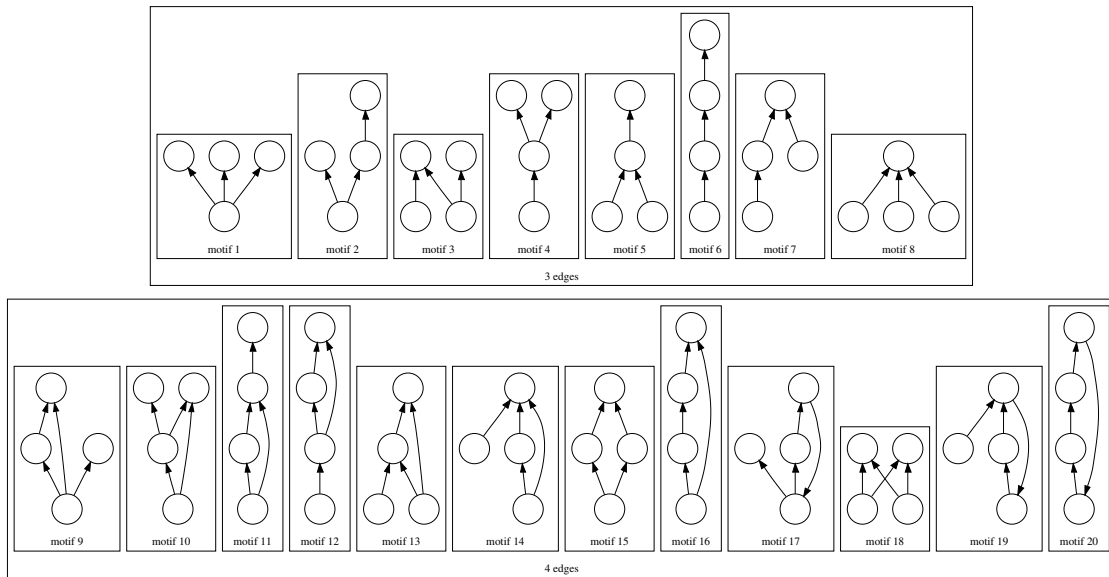


Fig. A2.— Diagrams of the 4-motifs with 3 and 4 edges. Circles are species and edges represent the flow of energy from one species to another.

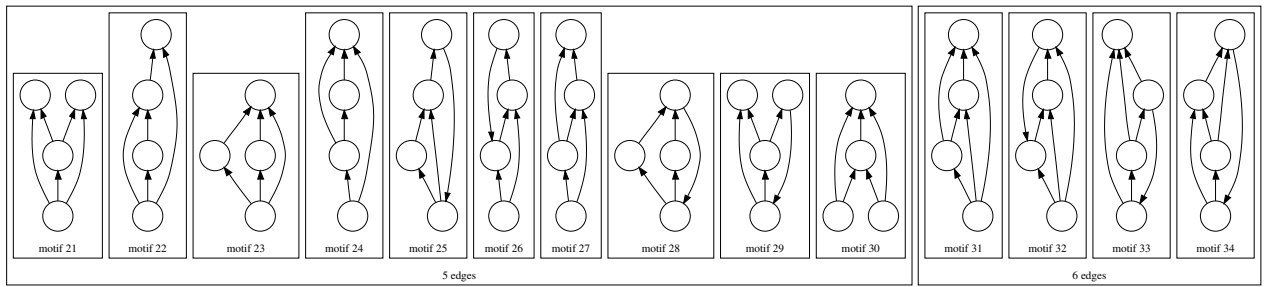


Fig. A3.— Diagrams of the 4-motifs with 5 and 6 edges. Circles are species and edges represent the flow of energy from one species to another.

Table A1—Continued

| Name | n | L | Control | | | | Impermanent | | | | Permanent | | | |
|------------|-----|-----|---------|---|----|---|-------------|---|----|---|-----------|---|----|---|
| | | | NC | | TC | | NC | | TC | | NC | | TC | |
| | | | – | + | – | + | – | + | – | + | – | + | – | + |
| | 32 | 4 | 5 | | | | | | | | | | | |
| | 33 | 4 | 5 | | | | | | | | | | | |
| 4-motif ID | 34 | 4 | 5 | | 5 | | | | | | | | | |

Note. — ‘NC’ are results from food webs with no trophic constraints, and ‘TC’ are results from food webs for which species were restricted in which trophic levels they could feed upon (see text). The NC webs were built with $f = 0.2$, and the TC webs with $f = 0.8$, which gives webs of similar connectance. Analysis is only performed on ‘large’ webs subject to their availability from each algorithm. So for NC webs from the control, impermanent and permanent algorithms respectively, motifs were calculated over 21 webs of size > 11 , 22 webs > 11 , and 21 webs > 11 . For TC webs, calculations were for 127 webs > 10 , 8 webs > 9 , and 23 webs > 10 .

A.3. Kirlinger’s method

Kirlinger (1986) showed that a web was permanent by demonstrating that, when each possible set of species was removed from the web, there was at least one positive transversal eigenvalue associated with that boundary fixed point. Loosely speaking, this is analogous to the test for invasion. When a single species attempts an invasion, it is successful when the transversal eigenvalue at the single boundary fixed point is greater than zero (Equation 2). Similarly, to ensure permanence, we must check that every boundary fixed point has at least one transversal eigenvalue greater than zero. In other words, we are testing that each subset of species can reinvade the system if their populations are brought arbitrarily close to zero.

The algorithm tested the reinvansion of each subset of species in order of increasing set size. So initially, it identified every species that could be removed from the web, testing that each species could reinvade. Then, for each of those species, it identified each additional species that could be removed with it, and the test was repeated, and so on. When a set of species was found that could not reinvade, it was removed, and the search was restarted. This was repeated until it was found that the entire web was permanent. Note that if the search reached a point where the web remaining after the removal of a subset was composed of either (1) isolated autotrophs or (2) feasible food chains, then that branch did not need to be tested further. This is because all such systems are permanent. The proof of this follows in Section A.4.

A.4. All feasible Lotka-Volterra food chains as defined in this paper are permanent

A.4.1. Definitions and notation

The food webs in this paper are governed by Lotka-Volterra dynamics,

$$\frac{dx_i}{dt} = x_i \left(d_i + \sum_{j=1}^n a_{i,j} x_j \right), \quad (\text{A1})$$

where x_i is the biomass of species i , d_i represents the intrinsic rate of increase of species i , and $a_{i,j}$ represents the interactions between a species i and another species j .

The following constraints are imposed upon the coefficients in Equation A1. A discussion of these assumptions may be found in Section 2.2.1 “Model Formulation”. For the intrinsic growth rate,

$$d_i > 0, \quad \text{if species } i \text{ is basal}; \quad (\text{A2})$$

$$d_i < 0, \quad \text{otherwise.} \quad (\text{A3})$$

For intraspecies interaction,

$$a_{i,i} < 0, \quad \text{if species } i \text{ is basal}; \quad (\text{A4})$$

$$a_{i,i} = 0, \quad \text{otherwise.} \quad (\text{A5})$$

And for interspecies interaction ($i \neq j$)

$$a_{i,j} > 0, \quad \text{if species } i \text{ predaes upon } j; \quad (\text{A6})$$

$$a_{i,j} < 0, \quad \text{if species } i \text{ is the prey of } j; \quad (\text{A7})$$

$$a_{i,j} = 0, \quad \text{if there is no relationship between species } i \text{ and } j. \quad (\text{A8})$$

Definition A.1. The *steady state biomass* of each species i , denoted x_i^* , is found by setting $\dot{x}_i = 0$ for all $i = 1, \dots, n$, where n is the number of species in the system.

Note that by the above definition, there is more than one steady state, because $x_i^* = 0$ is a valid steady state biomass for each species. Therefore, a food web is not only defined by its dynamical equations, but by which species are assumed present in the system.

Definition A.2. A *food web*, W_n , can be defined by the number of species in it, n , which species are assumed to be present when the steady state is solved, $[1, \dots, n]$, the species' interaction coefficients $a_{i,j}$, and the intrinsic growth rates d_i . This can be summarised in the tuple structure

$$W_n = ([1, \dots, n], \mathbf{A}, \mathbf{d}), \tag{A9}$$

where \mathbf{A} is the matrix of interaction coefficients, and \mathbf{d} the vector of intrinsic growth rates.

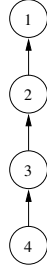


Fig. A4.— An example of a food chain.

Definition A.3. A *food chain* is a food web

$$C_n = ([1, \dots, n], \mathbf{A}, \mathbf{d}), \tag{A10}$$

in which

1. There is only one top species, with at most one prey;
2. There is only one basal species, with at most one predator; and
3. If there are any intermediate species, each of these species has only one predator and one prey.

Figure A4 shows an example of a food chain. It has a single basal species with one herbivore, a single top species with one prey, and all additional species have only one predator and one prey each. Thus it forms a ‘chain’ predator-prey interactions.

Note that Definition A.3 means that the structure of a food chain is uniquely defined by n , however there are many food chains with the same structure but different dynamics, as defined by \mathbf{A} and \mathbf{d} .

A single basal species is also included in the definition of food chains, as it satisfies the three conditions above – it is simply a ‘chain’ of one.

For the remainder of this Appendix, we restrict our interest to food chains. For convenience, we will define a consistent notation for the species as follows.

Definition A.4. A food chain that contains n species will have species with index $i = 1, \dots, n$ such that

1. The top species has index $i = 1$;
2. The basal species has index $i = n$;
3. The predator of species i has index $i - 1$; and
4. The prey of species i has index $i + 1$.

The example shown in Figure A4 conforms to this notation. This notation also simplifies \mathbf{A} and \mathbf{d} as shown below.

Corollary A.5. For a single basal species, $n = 1$, Equation A1 becomes

$$\dot{x}_1 = x_1 (d_1 + a_{1,1}x_1), \tag{A11}$$

and for a food chain with $n > 1$, Equation A1 becomes

$$\dot{x}_1 = x_1 (d_1 + a_{1,2}x_2), \quad \text{for the top predator;} \quad (\text{A12})$$

$$\dot{x}_i = x_i (d_i + a_{i,i-1}x_{i-1} + a_{i,i+1}x_{i+1}), \quad \text{for any intermediate species;} \quad (\text{A13})$$

$$\dot{x}_n = x_n (d_n + a_{n,n-1}x_{n-1} + a_{n,n}x_n), \quad \text{for the basal species.} \quad (\text{A14})$$

Definition A.6. A *subsystem*, S , is a food web in which not all of the species are present. It is evaluated by setting the steady state biomass of those species to zero.

$$S = W_n \setminus [i_1, \dots, i_k] = ([i_{k+1}, \dots, i_n], \mathbf{A}, \mathbf{d}). \quad (\text{A15})$$

Definition A.7. The *empty subsystem* is the empty food web that is formed by taking all species in a web and setting their steady state biomass to zero.

$$S = W_n \setminus [i_1, \dots, i_n] = (\emptyset, \mathbf{A}, \mathbf{d}). \quad (\text{A16})$$

A subsystem as defined above does not take into account the consequences of removing species on other species in the web. In certain cases, the removal of some species will cause other species to go extinct at steady state, or will cause the system to become singular so that no single steady state can be found. Both of these imply that not every food web formed by the removal of a set of species exists dynamically. For this reason, the definition that follows is useful.

Definition A.8. A *feasible subsystem* is a subsystem in which $x_i^* > 0$ for all species i in the subsystem.

For our food chains, the problem of defining subsystems simplifies somewhat; if a species goes extinct, all of the predators above it will also be driven to extinction. Therefore, if we only name those subsystems that have the potential to be feasible, then they can be named as defined below.

Definition A.9. For a food chain, S_k^n refers to the subsystem of C_n that is formed by setting $x_i^* = 0$ for species $1, \dots, k$, denoted

$$S_k^n = C_n \setminus [1, \dots, k] = ([k + 1, \dots, n], \mathbf{A}, \mathbf{d}). \quad (\text{A17})$$

For example, if a subsystem of C_4 , as shown in Figure A4, is formed by removing species 2, this also sends species 1 extinct. The subsystem resulting from this will be subsystem S_2^4 , which has species 3 as its top predator.

A.4.2. A sufficient condition for permanence

Definition A.10. The *transversal eigenvalues associated with S* are

$$\left. \frac{\dot{x}_i}{x_i} \right|_S = d_i + \sum_{j=1}^n a_{i,j} x_j^* \Big|_S, \text{ for } i \text{ in } W_n \setminus S. \quad (\text{A18})$$

The notation $x_j^* \Big|_S$ indicates that the biomass of species j is being evaluated at the steady state of the subsystem S , so

$$x_j^* = 0 \text{ for } j \text{ in } W_n \setminus S. \quad (\text{A19})$$

Lemma A.11. *For a food chain, when the notation in Definition A.4 is used, the transversal eigenvalues associated with S_k^n are of the form*

$$\left. \frac{\dot{x}_i}{x_i} \right|_{S_k^n} = d_i + a_{i,i+1} x_{i+1}^* \Big|_{S_k^n} + a_{i,i} x_i^* \Big|_{S_k^n} + a_{i,i-1} x_{i-1}^* \Big|_{S_k^n}, \text{ for } i = 1, \dots, k, \quad (\text{A20})$$

Further, because $x_i^* \Big|_{S_k^n} = 0$ for $i = 1, \dots, k$, then Equation A20 simplifies to

$$\left. \frac{\dot{x}_i}{x_i} \right|_{S_k^n} = \begin{cases} d_i, & \text{where } i < k; \\ d_k + a_{k,k+1} x_{k+1}^* \Big|_{S_k^n}, & \text{where } i = k \text{ and } k \neq n; \\ d_n, & \text{where } i = k = n. \end{cases} \quad (\text{A21})$$

As demonstrated in Kirlinger (1986), the permanence of a system can be established by testing the sign of the transversal eigenvalues associated with each subsystem. The definition below describes a sufficient condition for permanence. An very good explanation of the historical development of this condition along with references and proofs can be found in Chapter 4 of Cantrell & Cosner (2003).

Theorem A.12. *A food web is permanent if it has a feasible steady state, and for every feasible subsystem and for the empty subsystem, at least one transversal eigenvalue associated with that subsystem is positive.*

There are a number of ways to interpret Theorem A.12.

Finding the transversal eigenvalues associated with each subsystem is equivalent to checking each boundary steady state to see if it attracts or repels trajectories. The transversal eigenvalues can be thought of as the initial growth rates of species that have been brought very close to extinction. Thus, to test for at least one positive transversal eigenvalue is to test that this state of near-extinction is a repeller, and that the species that are near extinction can reinvade and reestablish themselves in the system.

Permanence requires that every boundary steady state is a repeller. So loosely speaking, it checks that for every set of species that comes close to extinction, those species can recover and reinvade the system.

A.4.3. Building the proof

Lemma A.13. *An isolated basal species is permanent.*

Proof. An isolated basal species is governed by the equation

$$\dot{x}_1 = x_1(d_1 + a_{1,1}x_1), \tag{A22}$$

with $d_1 > 0$ and $a_{1,1} < 0$. In order to demonstrate that this is permanent, we must demonstrate that it has a feasible steady state, and that every subsystem has at least one positive transversal eigenvalue.

First, we demonstrate that it has a feasible steady state. At steady state, Equation A22 rearranges to

$$x_1^* = \frac{-d_1}{a_{1,1}}. \quad (\text{A23})$$

As $-d_1 < 0$ and $a_{1,1} < 0$, this implies that $x_1^* > 0$, and thus the system has a feasible steady state.

Second, we demonstrate that every subsystem has at least one positive transversal eigenvalue. The only possible subsystem of an isolated autotroph is the empty system, so to show that the system is permanent, we only need to demonstrate that there is at least one positive transversal eigenvalue associated with this subsystem.

The empty subsystem, S_n^n has only one transversal eigenvalue, which is

$$\left. \frac{\dot{x}_1}{x_1} \right|_{S_n^n} = d_1 + a_{1,1} x_1^*|_{S_n^n}. \quad (\text{A24})$$

Therefore, in order to show that the system is permanent, we only need to demonstrate that this transversal eigenvalue is positive.

As $x_1^*|_{S_n^n} = 0$,

$$\left. \frac{\dot{x}_1}{x_1} \right|_{S_n^n} = d_1. \quad (\text{A25})$$

Since basal species have $d_i > 0$ by definition (Equation A2),

$$\left. \frac{\dot{x}_1}{x_1} \right|_{S_n^n} = d_1 > 0, \quad (\text{A26})$$

and thus, the system is permanent. □

Lemma A.14. *In order to establish the permanence of a feasible food chain with $n > 1$, we need only establish that*

$$\frac{\dot{x}_k}{x_k} \Big|_{S_k^n} = d_k + a_{k,k+1} x_{k+1}^* \Big|_{S_k^n} > 0, \text{ for all } k = 1, \dots, n-1. \quad (\text{A27})$$

Proof. This follows from a combination of Lemma A.11 and Lemma A.13.

Consider the most stringent case, which is that all subsystems S_k^n are feasible and therefore all must have their transversal eigenvalues tested. Then in order to establish permanence, we must show that at least one transversal eigenvalue associated with S_k^n for $k = 1, \dots, n$ is positive.

From Lemma A.11, the transversal eigenvalues associated with the empty subsystem, S_n^n are

$$\frac{\dot{x}_i}{x_i} \Big|_{S_n^n} = \begin{cases} d_i, & \text{where } i < n; \\ d_n, & \text{where } i = n. \end{cases} \quad (\text{A28})$$

From Equation A2, $d_n > 0$, thus subsystem S_n^n always has one positive transversal eigenvalue.

From Lemma A.11, the transversal eigenvalues associated with subsystems S_k^n for $k = 1, \dots, n-1$ are

$$\frac{\dot{x}_i}{x_i} \Big|_{S_k^n} = \begin{cases} d_i, & \text{where } i < k; \\ d_{k-1} + a_{k-1,k} x_k^* \Big|_{S_k^n}, & \text{otherwise (where } i = k). \end{cases} \quad (\text{A29})$$

Consider the first case in Equation A29. From Equation A2, $d_i < 0$ for all $i < n$. From the constraint above, $k = 1, \dots, n-1$ and all $i \leq k$ in Equation A29. Therefore, all $d_i < 0$ in Equation A29. This means that the transversal eigenvalue in the first case is always negative.

Now consider the second case in Equation A29. In this second case, d_{k-1} is also negative, however $a_{k-1,k} x_k^*$ may be positive, which may render this transversal eigenvalue positive. Therefore, in order to establish that the system is permanent, we need only demonstrate that the second case is positive for all subsystems $k = 1, \dots, n - 1$. \square

Lemma A.15. *For a food chain, S_k^n will have one positive transversal eigenvalue if and only if $x_{k+1}^*|_{S_k^n} > x_{k+1}^*|_{S_{k-1}^n}$.*

Proof. From Lemma A.14, there is only one transversal eigenvalue which may be positive, which is given in Equation A27. Rearranging it results in the following condition

$$x_{k+1}^*|_{S_k^n} > \frac{-d_k}{a_{k,k+1}}. \quad (\text{A30})$$

Conversely, if the inequality above is false, then the transversal eigenvalue will be negative.

The relationship in Equation A30 has the following interpretation. Consider the subsystem S_{k-1}^n , such that species k is the top predator. If this is the case, then the steady-state biomass of species $k + 1$ can be found by setting species k 's differential equation to zero. So

$$\dot{x}_k|_{S_{k-1}^n} = 0 = x_k^*|_{S_{k-1}^n} (d_k + a_{k,k+1} x_{k+1}^*|_{S_{k-1}^n}), \quad (\text{A31})$$

which implies that the steady-state biomass of species $k + 1$ in S_{k-1}^n is

$$x_{k+1}^*|_{S_{k-1}^n} = \frac{-d_k}{a_{k,k+1}}. \quad (\text{A32})$$

Equating Equation A30 and Equation A32 allows us to reinterpret the condition for a positive transversal eigenvalue,

$$x_{k+1}^*|_{S_k^n} > x_{k+1}^*|_{S_{k-1}^n}. \quad (\text{A33})$$

\square

Corollary A.16. *In order to establish the permanence of a feasible food chain, we only need to establish that*

$$x_{k+1}^*|_{S_k^n} > x_{k+1}^*|_{S_{k-1}^n} \text{ for all } k = 1, \dots, n-1. \quad (\text{A34})$$

This follows from Lemma A.14 and Lemma A.15.

Lemma A.17. *Let \mathbf{A} be the matrix of interspecies interaction coefficients $a_{i,j}$, and let \mathbf{d} be the vector of intrinsic growth rates d_i . Then for a feasible food chain, when a Gaussian Elimination is performed on the matrix $\mathbf{G}' = [\mathbf{A} | -\mathbf{d}]$ to obtain the lower triangular form of the matrix \mathbf{G} , all elements of \mathbf{G} have the same sign or are zero.*

Proof. Consider the first two steps of the Gaussian Elimination (GE) performed upon $\mathbf{G}' = [\mathbf{A} | -\mathbf{d}]$ starting from the bottom. The GE matrix at the start of the procedure is shown below.

$$\begin{pmatrix} \vdots \\ g'_{n-2} \\ g'_{n-1} \\ g'_n \end{pmatrix} = \begin{pmatrix} \vdots & & & & & & | & \vdots \\ 0 & \dots & a_{n-2,n-3} & 0 & a_{n-2,n-1} & 0 & | & -d_{n-2} \\ 0 & \dots & 0 & a_{n-1,n-2} & 0 & a_{n-1,n} & | & -d_{n-1} \\ 0 & \dots & 0 & 0 & a_{n,n-1} & a_{n,n} & | & -d_n \end{pmatrix},$$

We will use g'_i to refer to the i th row of \mathbf{G}' , and $g'_{i,j}$ to refer to the element at row i and column j of \mathbf{G}' . To get \mathbf{G}' into the lower triangular form \mathbf{G} , each of the $g'_{k,k+1}$ terms need to be set to zero. This is done by operations of the form

$$g_{k-1} = g'_{k-1} - g_k \frac{g'_{k-1,k}}{g_{k,k}}. \quad (\text{A35})$$

Note that this can be achieved in a single ‘sweep’ up the matrix.

Consider the first operation, starting from the bottom. The bottom row, g'_n , is already in its final form, so $g_n = g'_n$. Our objective is to get the $a_{n-1,n}$ term set to zero, so the

operation is $g_{n-1} = g'_{n-1} - g_n \frac{a_{n-1,n}}{a_{n,n}}$ (c.f. Equation A35), which results in

$$\left(g_{n-1} \right) = \left(0 \quad \dots \quad 0 \quad a_{n-1,n-2} \quad -\frac{(a_{n,n-1})(a_{n-1,n})}{a_{n,n}} \quad 0 \quad | \quad -d_{n-1} + d_n \frac{a_{n-1,n}}{a_{n,n}} \right). \quad (\text{A36})$$

Now we can show that each term in the modified second-from-bottom row has a negative sign.

Starting from the left,

$$g_{n-1,n-2} = a_{n-1,n-2} < 0, \quad (\text{A37})$$

because species $n - 2$ predates upon $n - 1$. Each of the terms in $-\frac{(a_{n,n-1})(a_{n-1,n})}{a_{n,n}}$ have the following signs:

$$a_{n,n} < 0, \quad (\text{A38})$$

$$a_{n-1,n} > 0, \quad (\text{A39})$$

$$a_{n,n-1} < 0, \quad (\text{A40})$$

so

$$g_{n-1,n-1} = -\frac{(a_{n,n-1})(a_{n-1,n})}{a_{n,n}} < 0. \quad (\text{A41})$$

Now consider solving for the steady-state using g_{n-1} . This results in

$$g_{n-1,n-2}x_{n-2}^* + g_{n-1,n-1}x_{n-1}^* = -d_{n-1} + d_n \frac{a_{n-1,n}}{a_{n,n}}. \quad (\text{A42})$$

Because we have assumed that the steady-state is feasible, Equations A37, A41, and the constraint $x_i^* > 0$ for all i implies that

$$-d_{n-1} + d_n \frac{a_{n-1,n}}{a_{n,n}} = g_{n-1,n+1} < 0. \quad (\text{A43})$$

So, after the first step, the last few rows of the GE matrix are

$$\begin{pmatrix} \vdots \\ g'_{n-2} \\ g_{n-1} \\ g_n \end{pmatrix} = \begin{pmatrix} \vdots & & & & & & | & \vdots \\ 0 & \dots & a_{n-2,n-3} & 0 & a_{n-2,n-1} & 0 & | & -d_{n-2} \\ 0 & \dots & 0 & g_{n-1,n-2} & g_{n-1,n-1} & 0 & | & g_{n-1,n+1} \\ 0 & \dots & 0 & 0 & a_{n,n-1} & a_{n,n} & | & -d_n \end{pmatrix},$$

with all $g_{n-1} \leq 0$. The second step results in

$$\left(g_{n-2} \right) = \left(0 \quad \dots \quad a_{n-2,n-3} \quad -\frac{(g_{n-1,n-2})(a_{n-2,n-1})}{g_{n-1,n-1}} \quad 0 \quad 0 \quad | \quad g_{n-2,n+1} \right), \quad (\text{A44})$$

where again, by similar reasoning, all $g_{n-2} \leq 0$. As operations of this form are continued up the matrix, each $g_{i,j}$ term will be either zero or negative. Thus the GE matrix in its final lower triangular form will have all negative elements, or elements of the same sign. \square

The completed Gaussian Elimination upon a food chain will have the following form

$$\begin{pmatrix} g_1 \\ g_2 \\ g_3 \\ g_4 \\ \vdots \\ g_{n-1} \\ g_n \end{pmatrix} = \begin{pmatrix} g_{1,1} & 0 & 0 & 0 & \dots & 0 & 0 & 0 & | & g_{1,n+1} \\ g_{2,1} & g_{2,2} & 0 & 0 & \dots & 0 & 0 & 0 & | & g_{2,n+1} \\ 0 & g_{3,2} & g_{3,3} & 0 & \dots & 0 & 0 & 0 & | & g_{3,n+1} \\ 0 & 0 & g_{4,2} & g_{4,4} & \dots & 0 & 0 & 0 & | & g_{3,n+1} \\ \vdots & & & & & & & & | & \vdots \\ 0 & 0 & 0 & 0 & \dots & g_{n-1,n-2} & g_{n-1,n-1} & 0 & | & g_{n-1,n+1} \\ 0 & 0 & 0 & 0 & \dots & 0 & g_{n,n-1} & g_{n,n} & | & g_{n,n+1} \end{pmatrix}, \quad (\text{A45})$$

where all nonzero elements $g_{i,j}$ have the same sign.

Corollary A.18. *For a food chain, the lower triangular Gaussian Elimination matrix for subsystem S_k^n can be obtained from the lower triangular Gaussian Elimination matrix for the original system by simply removing all rows and columns 1 to k .*

This can be seen by observing that in the discussion above, the lower triangular form was obtained by moving up the matrix in a single sweep without rearranging the rows or

columns. Thus, for subsystem S_{k-1}^n , Equation A45 becomes

$$\begin{pmatrix} g_k \\ g_{k+1} \\ g_{k+2} \\ \vdots \\ g_{n-1} \\ g_n \end{pmatrix} = \begin{pmatrix} g_{k,k} & 0 & 0 & \dots & 0 & 0 & 0 & | & g_{k,n+1} \\ g_{k+1,k} & g_{k+1,k+1} & 0 & \dots & 0 & 0 & 0 & | & g_{k+1,n+1} \\ 0 & g_{k+2,k} & g_{k+2,k+2} & \dots & 0 & 0 & 0 & | & g_{k+2,n+1} \\ \vdots & & & & & & & | & \vdots \\ 0 & 0 & 0 & \dots & g_{n-1,n-2} & g_{n-1,n-1} & 0 & | & g_{n-1,n+1} \\ 0 & 0 & 0 & \dots & 0 & g_{n,n-1} & g_{n,n} & | & g_{n,n+1} \end{pmatrix}, \quad (\text{A46})$$

with all g terms the same as in Equation A45.

Lemma A.19. *For any subsystem S_{k-1}^n of a feasible food chain, $x_k^*|_{S_{k-1}^n} > x_k^*|_{C_n}$, which ensures that $x_k^*|_{S_{k-1}^n} > 0$.*

Proof. The Gaussian Elimination performed Lemma A.17 gives the following equation for solving the steady-state of species k in the original chain

$$g_{k,k-1} x_{k-1}^*|_{C_n} + g_{k,k} x_k^*|_{C_n} = g_{k,n+1}, \quad (\text{A47})$$

where all $g_{i,j}$ terms have the same sign.

From Corollary A.18, when subsystem S_{k-1}^n is formed such that species k is the top predator and all species $1 \dots k-1$ are removed, Equation A47 becomes

$$g_{k,k} x_k^*|_{S_{k-1}^n} = g_{k,n+1}. \quad (\text{A48})$$

As all g terms in Equation A48 are the same as in Equation A47, this implies

$$g_{k,k} x_k^*|_{S_{k-1}^n} = g_{k,k} x_k^*|_{C_n} + g_{k,k-1} x_{k-1}^*|_{C_n}. \quad (\text{A49})$$

Because we imposed the constraint $x_j^*|_{C_n} > 0$, and because all g terms have the same sign, this implies

$$x_k^*|_{S_{k-1}^n} > x_k^*|_{C_n}. \quad (\text{A50})$$

Thus we are assured if the original system is feasible, which implies that $x_k^*|_{C_n} > 0$, then $x_k^*|_{S_{k-1}^n} > 0$. \square

Note that Lemma A.19 does not say that any subsystem S_{k-1}^n is feasible, only that the top predator in the system will have a positive steady state.

Lemma A.20. *For a feasible food chain, $x_{k+1}^*|_{S_k^n} > x_{k+1}^*|_{S_{k-1}^n}$ for all $k = 1, \dots, n - 1$.*

Proof. This is demonstrated similar to Lemma A.19. In subsystem $k - 1$,

$$g_{k+1,k} x_k^*|_{S_{k-1}^n} + g_{k+1,k+1} x_{k+1}^*|_{S_{k-1}^n} = g_{k+1,n+1}, \quad (\text{A51})$$

and in subsystem k

$$g_{k+1,k+1} x_{k+1}^*|_{S_k^n} = g_{k+1,n+1}. \quad (\text{A52})$$

From Corollary A.18, we know that all of the $g_{i,j}$ terms in Equation A52 are the same as in Equation A51, therefore the two equations can be equated to give

$$g_{k+1,k+1} x_{k+1}^*|_{S_k^n} = g_{k+1,k} x_k^*|_{S_{k-1}^n} + g_{k+1,k+1} x_{k+1}^*|_{S_{k-1}^n}. \quad (\text{A53})$$

We imposed the constraint that the full system was feasible, and from Lemma A.19 we know that this implies $x_k^*|_{S_{k-1}^n} > 0$. Therefore Equation A53 implies

$$x_{k+1}^*|_{S_k^n} > x_{k+1}^*|_{S_{k-1}^n}. \quad (\text{A54})$$

\square

Corollary A.21. *Every feasible food chain is permanent.*

This follows from Corollary A.16 and Lemma A.20.

A.5. Heterotrophs in permanent webs are more efficient

The dynamical constraints upon the food webs prevented some species from invading and caused others to go extinct, changing the autotroph intrinsic growth rate, d_i , heterotroph interaction coefficient, $-a_{j,i}$, and efficiency $a_{i,j}/-a_{j,i}$, compared to the standard uniform distributions from which they were chosen (Table A2). For both permanent and impermanent feasible webs, the dynamical constraints select for basal species with significantly higher intrinsic growth rate, and for heterotrophs with significantly higher interaction coefficient and efficiency (Table A2).

When the results from permanent and impermanent webs are compared, the mean value of $-a_{j,i}$ is not significantly different ($t = 0.6099$, d.f. = 2189.998, $P = 0.542$), but the mean efficiency of heterotrophs in permanent webs was significantly higher than in impermanent webs ($t = 5.9451$, d.f. = 2180.915, $P < 0.001$), and the mean intrinsic growth rate of autotrophs was greater in permanent webs than in impermanent webs with $P = 0.007$ ($\bar{x}_1 = 0.71$, $\bar{x}_2 = 0.67$, $t = 2.4809$, d.f. = 815.741).

Table A2. Statistical properties of a comparison between species in permanent and impermanent feasible webs and the random standard uniform distribution from which all new species were generated.

| Algorithm | Statistics | d_i | $-a_{j,i}$ | $a_{i,j}/-a_{j,i}$ |
|----------------------|--------------|--------|------------|--------------------|
| Permanent | Sample size | 431 | 1097 | 1097 |
| | KS test: D | 0.3152 | 0.0902 | 0.1723 |
| | T-test: mean | 0.71 | 0.56 | 0.61 |
| Impermanent feasible | Sample size | 408 | 1095 | 1095 |
| | KS test: D | 0.2602 | 0.1723 | 0.0657 |
| | T-test: mean | 0.67 | 0.55 | 0.54 |

Note. — Coefficient values taken from 189 permanent webs and 144 impermanent feasible webs. Species characteristics are autotroph intrinsic growth rate, d_i , heterotroph interaction coefficient, $-a_{j,i}$, and efficiency $a_{i,j}/-a_{j,i}$. A Kolmogorov-Smirnov (KS) test is used to compare the distribution of the characteristics to a standard uniform distribution, where D is the test statistic. A one-sided t-test is used to compare the characteristics' means to the expected value from a standard uniform distribution. All tests resulted in $P < 0.001$.

The question may be asked, how much of the difference in attributes between permanent to impermanent webs is because of the constraint applying at that particular point in time, and how much of it accumulates over the history of the web? To answer this, for each impermanent web, species were removed until a permanent subsystem was found. A comparison was made between permanent webs, impermanent webs, and the permanent subsystems of the impermanent webs. This revealed that the difference between permanent and impermanent webs is a combination of both the constraint acting at that particular time and its effect over the history of the assembly process. Specifically, impermanent webs had a lower efficiency than their permanent subsystems with $P = 0.004$ ($\bar{x}_1 = 0.58, \bar{x}_2 = 0.54, t = 2.6662, \text{d.f.} = 1353.901$), however the efficiency of the subsystems was still lower than permanent webs created with the permanence algorithm, with $P = 0.007$ ($\bar{x}_1 = 0.58, \bar{x}_2 = 0.61, t = 2.4446, \text{d.f.} = 1265.447$). Similarly, the mean d_i value increased from 0.67 for impermanent webs to 0.68 for permanent webs, reducing the P-value of the one-tailed test to 0.048 ($t = 1.6666, \text{d.f.} = 688.644$).

A.6. Supplementary tables and figures

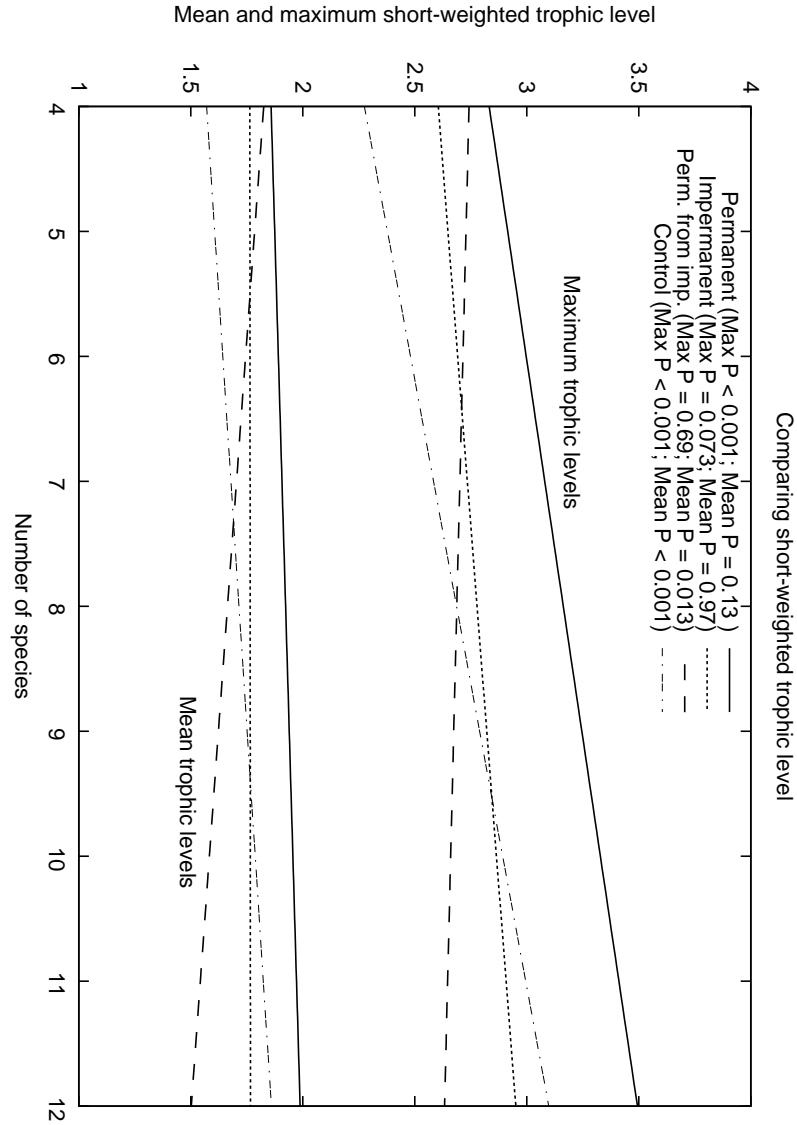


Fig. A5.— Linear regressions on the short-weighted mean and maximum trophic level against food web size between 4 and 12, with P-values quoted for the significance level of the slope coefficient. The regression equations are as follows: mean control $y = 1.4 + 0.04n$, maximum control $y = 1.9 + 0.10n$, mean permanent $y = 1.8 + 0.02n$, maximum permanent $y = 2.5 + 0.08n$, mean impermanent $y = 1.8 + 0.0003n$, maximum impermanent $y = 2.4 + 0.04n$.

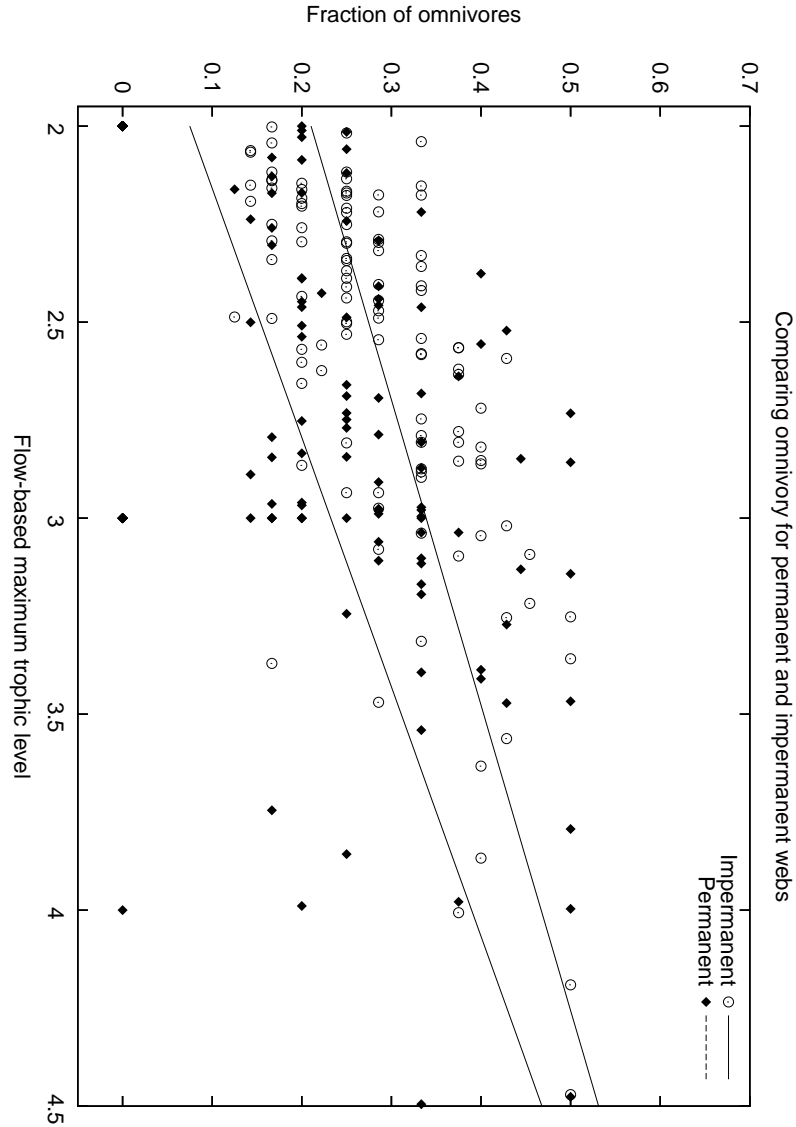


Fig. A6.— Linear regressions ($P < 0.001$) and data for the fraction of omnivores in each web against the food web’s trophic height (measured as maximum flow-based trophic level). A species interaction probability of $f = 0.8$ was used. Note that in the figure above, there are 16 permanent food webs out of 116 food webs with flow-based trophic height greater than 2 that contain no omnivores. This is in contrast to 110 impermanent webs of height greater than 2, for which none contained no omnivores. Similar results are obtained for $f = 0.2$: 48 out of 154 permanent webs (with trophic height greater than 2) contained no omnivores,

Table A3. Multinomial regression equations applied to output from each of the food web building algorithms and to data from the literature.

| Attribute | Modelled on | Regression logit $\hat{p} =$ | P-value for slope coefficient |
|--------------------------------|-------------|------------------------------|-------------------------------|
| Control, 179 webs | | | |
| T | T,I | $-0.206 - 0.0894n$ | $P < 0.01$ |
| I | I,T | $-1.983 + 0.1341n$ | $P < 0.01$ |
| B | B,T | $0.337 - 0.0774n$ | $P < 0.01$ |
| Engaged links | | $-0.485 - 0.0452n$ | $P < 0.01$ |
| Permanent, 189 webs | | | |
| T | T,I | $-0.299 - 0.0864n$ | $P < 0.01$ |
| I | I,T | $-1.524 + 0.1103n$ | $P < 0.01$ |
| B | B,T | $-0.237 - 0.0333n$ | $P = 0.011$ |
| Engaged links | | $0.545 - 0.1607n$ | $P < 0.01$ |
| Feasible all, 130 webs | | | |
| T | T,I | $-0.147 - 0.0991n$ | $P < 0.01$ |
| I | I,T | $-2.613 + 0.2287n$ | $P < 0.01$ |
| B | B,T | $0.298 - 0.0995n$ | $P < 0.01$ |
| Engaged links | | $1.321 - 0.2681n$ | $P < 0.01$ |
| Feasible impermanent, 144 webs | | | |
| T | T,I | $-0.897 - 0.0323n$ | $P = 0.11$ |
| I | I,T | $-0.701 + 0.0073n$ | $P = 0.70$ |
| B | B,T | $-0.483 + 0.0177n$ | $P = 0.32$ |
| Engaged links | | $1.385 - 0.2504n$ | $P < 0.01$ |
| Havens (1992), 50 webs | | | |

Table A3—Continued

| Attribute | Modelled on | Regression logit $\hat{p} =$ | P-value for slope coefficient |
|---|-------------|------------------------------|-------------------------------|
| T | T,I | $-2.126 - 0.0178n$ | $P = 0.031$ |
| I | I,T | $-0.746 + 0.0125n$ | $P = 0.022$ |
| B | B,T | $0.217 - 0.0057n$ | $P = 0.118$ |
| Engaged links | | $-1.266 - 0.00194n$ | $P = 0.45$ |
| All Schoenly et al. (1991) data, 61 webs | | | |
| T | T,B | $-0.356 + 0.0064n$ | $P = 0.114$ |
| I | I,B | $-0.377 + 0.0012n$ | $P = 0.767$ |
| B | B,T | $-1.160 - 0.0281n$ | $P < 0.01$ |
| Engaged links | | $-0.606 - 0.0300n$ | $P < 0.01$ |
| Schoenly et al. (1991) phytotelmata data, 15 webs | | | |
| T | T,I | $0.522 - 0.0860n$ | $P = 0.085$ |
| I | I,T | $-2.833 + 0.1750n$ | $P < 0.01$ |
| B | B,T | $0.192 - 0.0985n$ | $P = 0.068$ |
| Schoenly et al. (1991) carrion data, 13 webs | | | |
| T | T,I | $2.361 - 0.0718$ | $P < 0.01$ |
| I | I,T | $-2.780 + 0.0694$ | $P < 0.01$ |
| B | B,T | $-3.507 + 0.0362$ | $P = 1$ |