

Appendix A. Calculating the weighted-predictions matrix of loop analysis.

Loop analysis refers to a method of qualitative modeling developed by Richard Levins (Levins 1974, Levins 1975, Puccia and Levins 1985). Although the term “loop analysis” is no longer preferable due to the historical precedent of referring to loops as cycles (Dambacher et al. 2002), the term remains widely used for lack of a suitably specific alternative (Justus 2005, Justus 2006).

As illustrated by Dambacher et al. (2002), the classical adjoint of a matrix (a.k.a. its adjugate) is related to its inverse by its determinant such that

$$\text{adj}(-{}^\circ\mathbf{A}) = -{}^\circ\mathbf{A}^{-1} \cdot \det(-{}^\circ\mathbf{A}).$$

Both reflect the net effect of all feedback loops between each pair of species. The determinant of matrix \mathbf{A} can be expressed using the Leibniz formula,

$$\det(\mathbf{A}) = \sum_{\sigma} \text{sign}(\sigma) \prod_{i=1}^S \alpha_{i,\sigma(i)},$$

where the summation is over all σ possible matrix minors (all permutations of \mathbf{A} where one row and one column are each dropped) and $\text{sign}(\sigma)$ is -1 when the i^{th} of S total species in the community is an odd number and 1 when it is even. Calculating the inverse of a qualitatively-specified matrix requires that no two species have an identical linkage structure (e.g., the same predators and prey); the matrix will be singular otherwise {Searle, 1966 #243}. Such groups of aggregated trophic species are assumed *a priori* to have equivalent perturbation responses.

Dambacher et al. (2002) suggest that the ratio between the absolute net effect of all feedback loops (i.e. $|\text{adj}({}^\circ\mathbf{A})|$) and the total number of all complementary feedback loops affecting a given species pair can be used to gauge the reliability of how species i is predicted to respond to a positive change in j . The weighted-predictions matrix \mathbf{W} that embodies this notion is calculated as

$$\mathbf{W} = \frac{\overrightarrow{|\text{adj}({}^\circ\mathbf{A})|}}{\mathbf{T}} = |\text{adj}({}^\circ\mathbf{A})| \circ \mathbf{T}^+$$

with $w_{ij} = 0$ if $T_{ij} = 0$, where $|\text{adj}({}^\circ\mathbf{A})|$ indicates the absolute of the adjoint, the vector “ \rightarrow ” and the Hadamard product \circ respectively indicate element-wise division and multiplication, and \mathbf{T}^+ is the pseudo-inverse of the feedback matrix \mathbf{T} . This results in each element of \mathbf{W} being the absolute value of each ij element of the adjoint divided by the total number of feedback loops contributing to it.

The absolute feedback matrix \mathbf{T} is calculated by converting each element of ${}^\circ\mathbf{A}$ to its absolute value, applying the matrix permanent (a.k.a. the plus determinant) to each of the S^2 minors of the resulting matrix, and transposing the result. The matrix permanent is calculated by

$$\text{perm}(\mathbf{A}) = \sum_{\sigma} \prod_{i=1}^S \alpha_{i,\sigma(i)},$$

differing from the matrix determinant only in that the signs of the minors are dropped such that all terms are added. Lacking the symmetry of the determinant the calculation of the permanent is the computational crux to estimating the reliability scores of the weighted-prediction matrix. It remains a computationally intense problem: the most efficient algorithm for calculating the permanent exactly requires a minimum of $S^2 S$ arithmetic calculations for a matrix of S species (Ryser 1963), which must be repeated S^2 times to compute the absolute feedback matrix (see also Jerrum et al. 2004 for an approximate method).

LITERATURE CITED

- Dambacher, J. M., H. W. Li, and P. A. Rossignol. 2002. Relevance of community structure in assessing indeterminacy of ecological predictions. *Ecology* **83**:1372-1385.
- Dambacher, J. M., H. W. Li, and P. A. Rossignol. 2003. Qualitative predictions in model ecosystems. *Ecological Modelling* **161**:79-93.
- Jerrum, M., A. Sinclair, and E. Vigoda. 2004. A polynomial-time approximation algorithm for the permanent of a matrix with nonnegative entries. *J. ACM* **51**:671-697.
- Justus, J. 2005. Qualitative scientific modeling and loop analysis. *Philosophy of Science* **72**:1272-1286.
- Justus, J. 2006. Loop analysis and qualitative modeling: limitations and merits. *Biology and Philosophy* **V21**:647-666.
- Levins, R. 1974. The qualitative analysis of partially specified systems. *Annals of the New York Academy of Sciences* **231**:123-138.
- Levins, R. 1975. Evolution in communities near equilibrium. *in* M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap Press, Cambridge, MA.
- Puccia, C. J. and R. Levins. 1985. *Qualitative Modeling of Complex Systems: An Introduction to Loop Analysis and Time Averaging*. Harvard University Press, Cambridge.
- Ryser, H. J. 1963. *Combinatorial Mathematics*. Mathematical Association of America, New York.

Appendix B. The topological properties of the empirical food webs, and comparisons of qualitative versus quantitative predictions, aggregated versus non-aggregated food webs, and alternative parameterizations and richness-connectance levels.

Table B.1. Properties of the analyzed empirical food webs, ordered by the proportion of predictions made correctly by loop analysis. See Dunne *et al.* (2002, 2004, #1, 2) for further network properties.

Food web	Non-aggregated				Aggregated						Ref.
	S^1	L^2	C_I^3	C_d^4	S^1	L^2	R^5	C_I^3	C_d^4	% Correct predictions ⁷	
Canton Creek	108	707	0.06	0.07	102	696	0	0.07	0.08	0.60	#3
Ythan Estuary (with parasites)	134	594	0.03	0.04	82	391	1	0.06	0.07	0.57	#4
Ythan Estuary	92	417	0.05	0.06	82	391	1	0.06	0.07	0.56	#5
Chesapeake Bay	33	71	0.07	0.10	31	67	0	0.07	0.10	0.56	#6
Scotch Broom	154	366	0.02	0.02	85	219	0	0.03	0.04	0.55	#7
Bridge Brook Lake	75	548	0.10	0.11	25	104	1	0.17	0.20	0.51	#8
Stony Stream	112	830	0.07	0.08	109	827	0	0.07	0.08	0.51	#3
Benguela	29	196	0.24	0.26	29	196	5	0.24	0.26	0.50	#9
Skipwith Pond	35	369	0.30	0.32	25	189	4	0.31	0.34	0.50	#10
NE Shelf	81	1458	0.22	0.23	79	1378	7	0.22	0.23	0.50	#11
Grassland	75	113	0.02	0.03	61	97	0	0.03	0.04	0.50	#12
Caribbean Reef	50	535	0.21	0.22	50	535	32	0.21	0.22	0.50	#13
St. Martin Island	44	218	0.12	0.14	42	205	0	0.12	0.14	0.50	#14
Little Rock Lake	181	2358	0.07	0.08	92	984	24	0.11	0.12	0.50	#15
El Verde Rainforest	156	1508	0.06	0.07	155	1507	69	0.06	0.07	0.50	#16
St. Marks Seagrass	48	218	0.10	0.12	48	218	0	0.10	0.12	0.50	#17
Coachella Valley	30	270	0.28	0.30	29	243	22	0.27	0.30	0.50	#18

¹ S refers to the number of network nodes (species or aggregated trophic groups).

² L refers to number of pairwise interspecific links only.

³ C_I refers to interactive connectance.

⁴ C_d refers to directed connectance.

⁵ R refers to the number of species pairs exhibiting reciprocal predation in the original food web compilation.

⁶ Necessary condition for matrix inversion (see Appendix S1).

⁷ As calculated by loop analysis and depicted in Figure 1.

Note: Indices 1-4 & 6 calculated using the qualitatively specified community matrix with self-limitation in all species rather than the original list of observed pairwise trophic interactions.

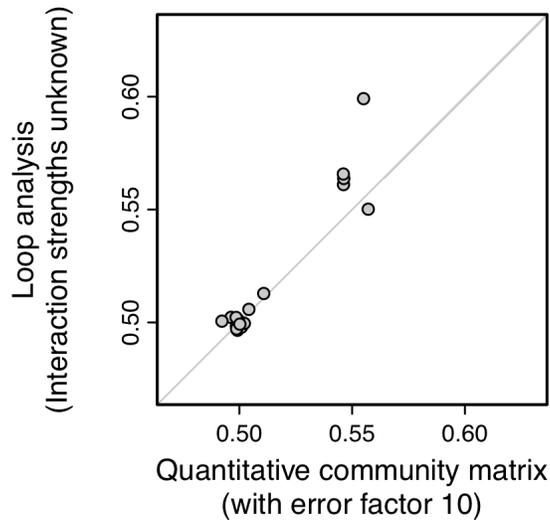


Figure B.1 Correspondence in the empirical food webs between the proportion of correct predictions made by loop analysis (when interaction strengths are unknown), and those made by using the quantified community matrix when interaction strengths are estimated to within an order of magnitude as in Figure 1a ($r^2 = 0.95$, $t = 12.3$ $df = 15$, $p \ll 0.001$). Line indicates 1:1 correspondence.

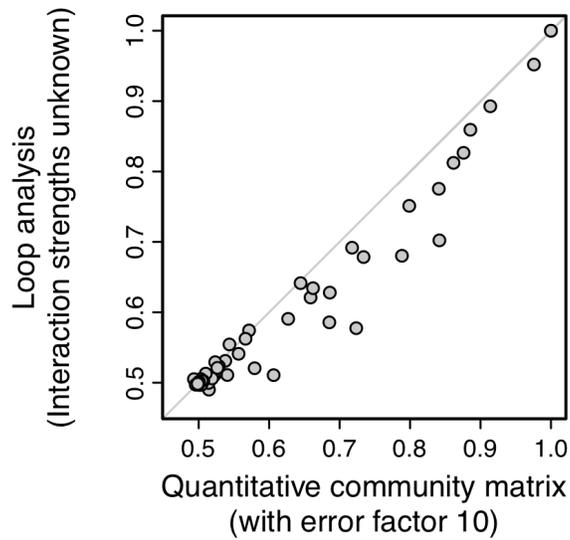


Figure B.2. Correspondence in the niche model food webs between the proportion of correct predictions made by loop analysis (when interaction strengths are unknown), and those made by using the quantified community matrix when interaction strengths are estimated to within an order of magnitude ($r^2 = 0.95$, $p \ll 0.001$). Line indicates 1:1 correspondence.

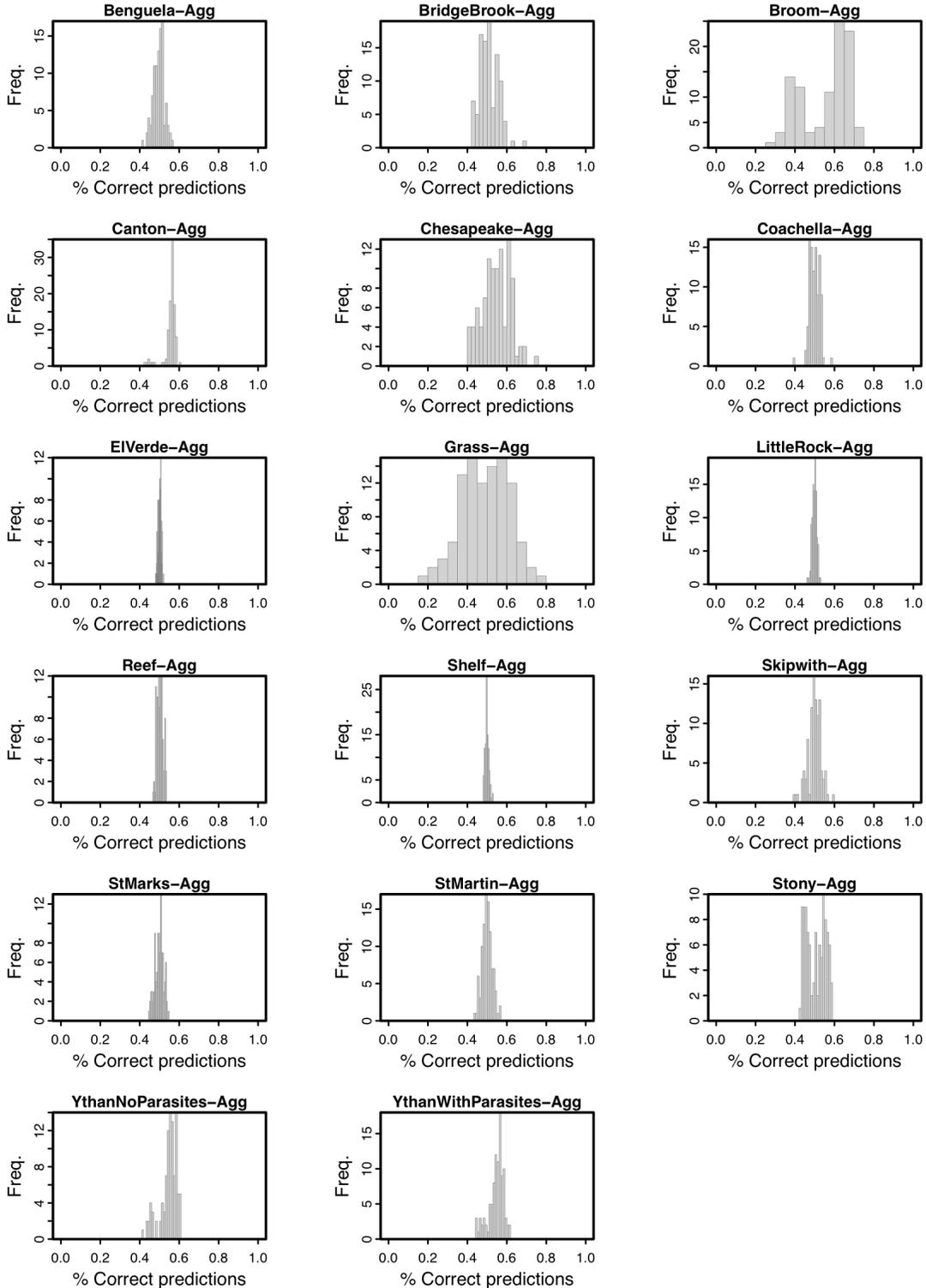


Figure B.3. Frequency histograms of the proportion of correct predictions made across 100 replicate interaction strength realizations of each network’s quantified community matrix when interaction strengths estimated to within an order of magnitude error ($F = 10$). The means of these distributions correspond to the means presented in Fig. 1. The 95th quantile of these distributions correspond to the proportion of correct predictions presented in Figure B.4.

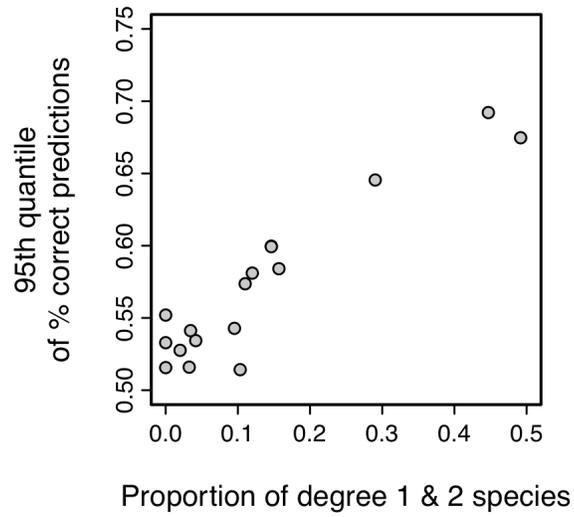


Figure B.4. Across all 17 empirical food webs, the upper 95th quantile of the proportion of correct predictions made using the quantified community matrix (with interaction strengths estimated to within an order of magnitude, $F = 10$) is well-explained by the proportion of species in the food web that are connected to only one or two other species ($r^2 = 0.93$, $t = 10.20$, $df = 15$, $p \ll 0.001$).

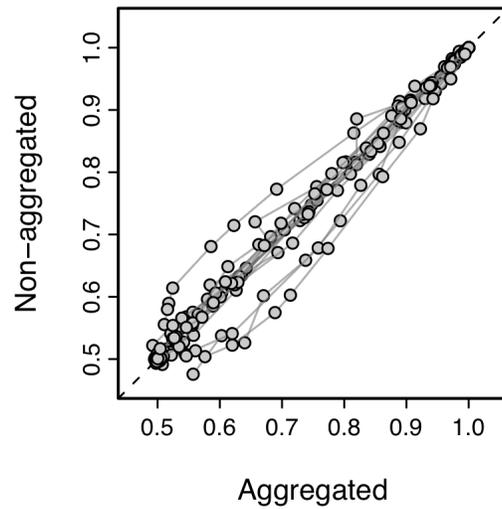


Figure B.5. The relationship between the mean predictive success of aggregated and non-aggregated empirical food webs. Connected points correspond to each of the 17 empirical food webs across successive levels of interaction strength estimation error. The main text presented analyses performed on webs of aggregated trophic species (species sharing identical predators and prey). This was necessary to permit comparisons between the predictive success of quantitative and qualitative approaches (see Appendix S1), but could reduce the topological indeterminacy of these networks to affect higher observed predictive success. The only web for which this was consistently not the case was Bridge Brook Lake, the most highly aggregated food web (Table S2.1), suggesting a trade-off between perceived predictive accuracy and the degree to which species are perceived to share the same sets of predators and prey.

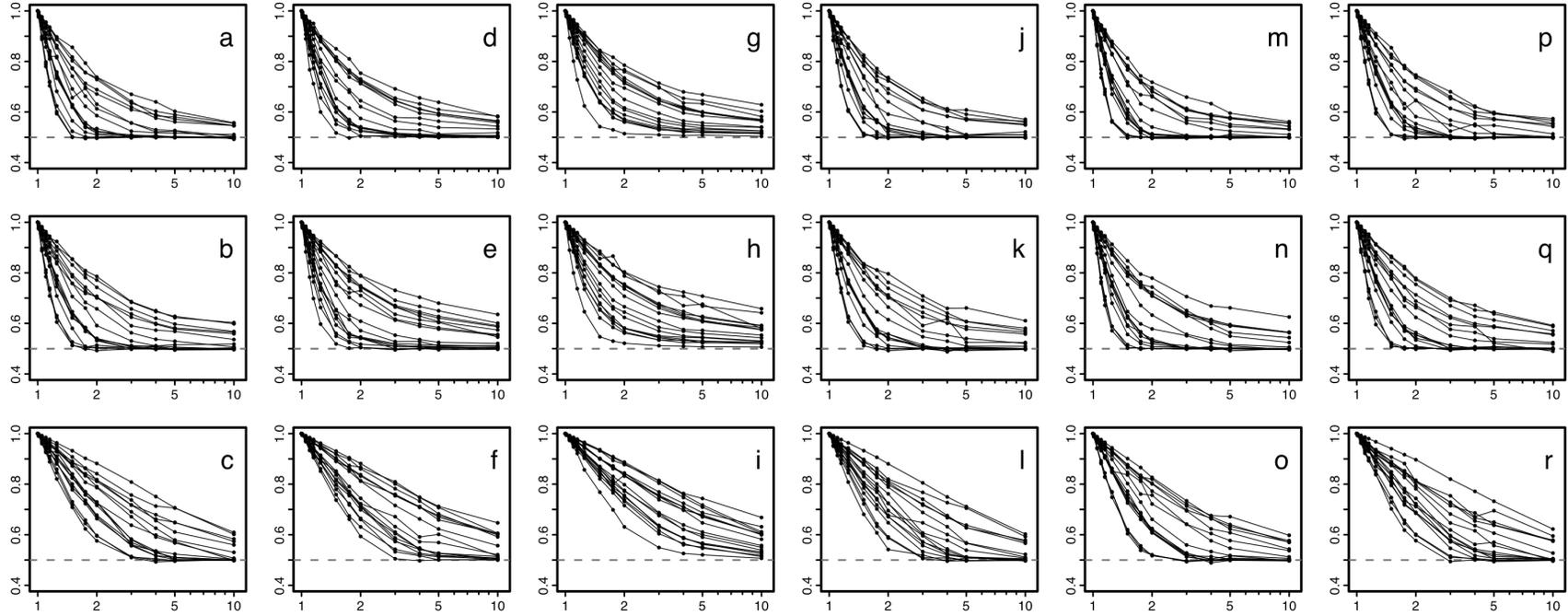


Figure B.6. Sensitivity of results to chosen interaction strength parameters. The mean proportion of correctly made qualitative predictions of species responses declines as a function of the error by which hypothetical interspecific interaction strengths are estimated in 17 well-characterized empirical food webs with parameters (a-c) $e = 0.1$, $a_{ij} > \text{basal} - a_{ii} = -1$, and a skewed Beta[1,4] distribution as in Figure 1, (d-f) $e = 0.5$, (g-i) $e = 0.9$, (j-l) $a_{ij} > \text{basal} - a_{ii} = -10$, (m-o) a uniform Beta[1,1] distribution, and (p-r) a more strongly skewed Beta[1,6] distribution. The rate of decline observed when all interactions are estimated with equal likelihood of error (top row) is affected little when only the weakest interactions are estimated accurately (middle row), but decreases when the strongest interactions are measured accurately (bottom row). An error factor of 1 corresponds to no estimation error, while an error factor of 10 corresponds to interaction strengths being estimated to within an order of magnitude for all interaction (top row), for only the strongest interactions (middle row), or for only the weakest interactions (bottom row). A proportion of 0.5 corresponds to a predictive ability matching that of flipping a coin.

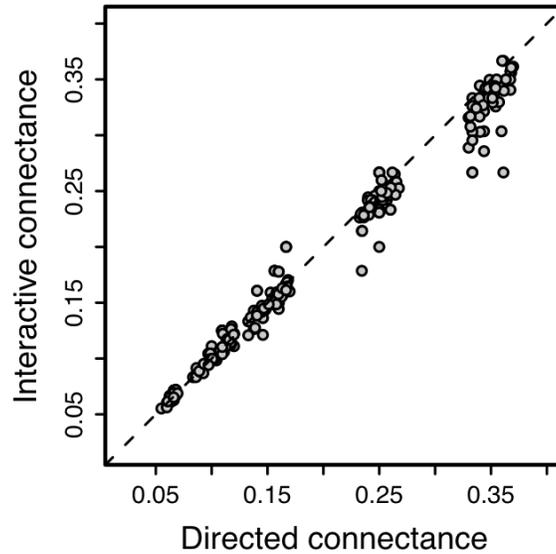


Figure B.7. To avoid the potential confusion introduced by assigning self-limitation effects to all species we illustrate the correspondence between the directed connectance (C_d) by which the complexity of the niche model food webs was specified and the interactive connectance (C_I) of their corresponding community matrices. The niche model uses directed connectance ($C_d = L/S^2$, where L is the total desired number of interspecific and cannibalistic self-limitation links), while interactive connectance counts interspecific links only ($C_I = L_I/S(S-1)$). Dashed line indicates 1:1 correspondence.

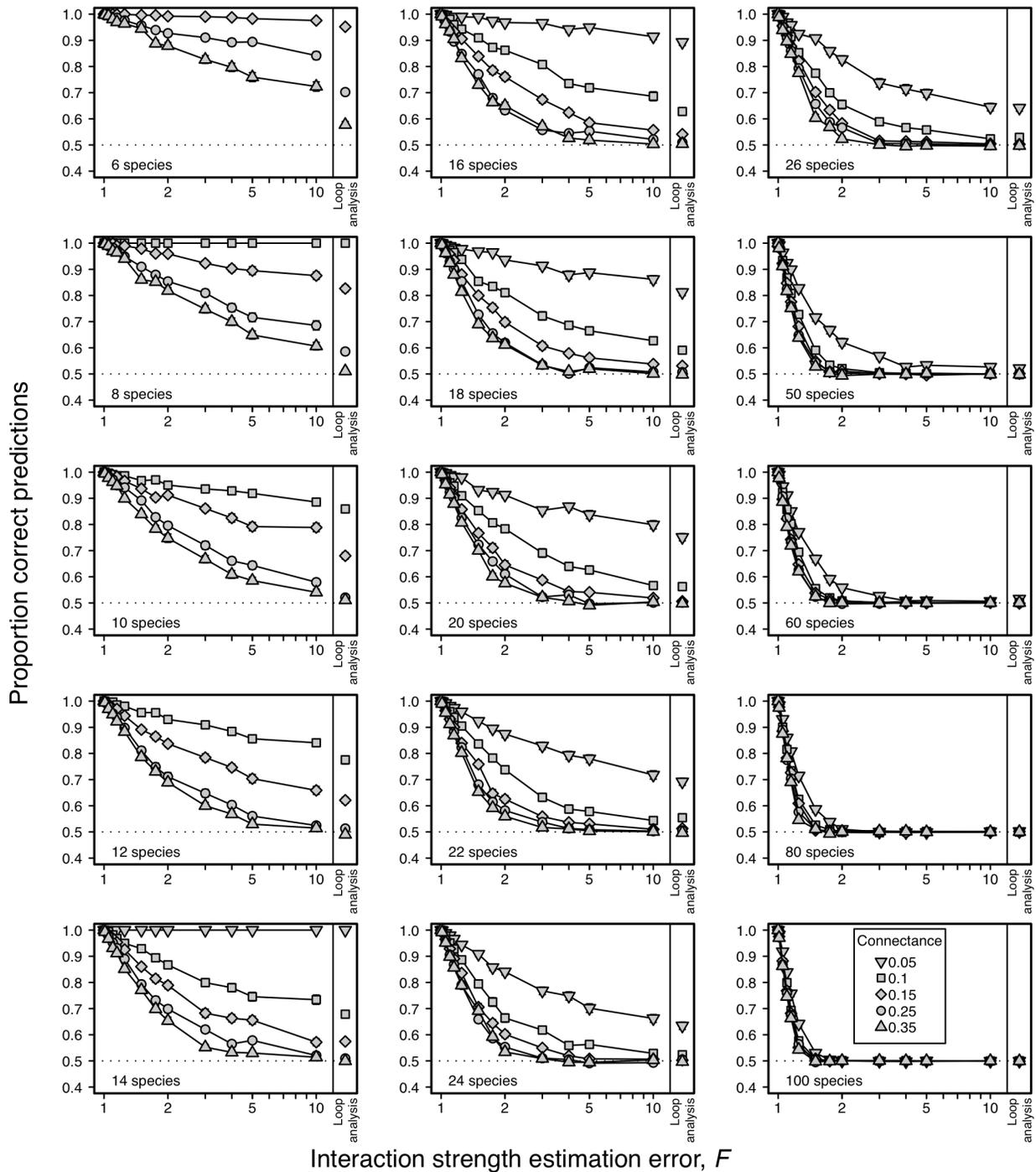


Figure B.8. The mean proportion of correctly made qualitative predictions of species responses as a function of the error by which interspecific interaction strengths are estimated in model communities of increasing size and complexity. An error factor of 1 corresponds to no estimation error, while an error factor of 10 corresponds to interaction strengths being estimated to within an order-of-magnitude for all interactions. Loop analysis uses network topology alone, assuming no knowledge of interaction strengths. Note the log-scale of the abscissa.

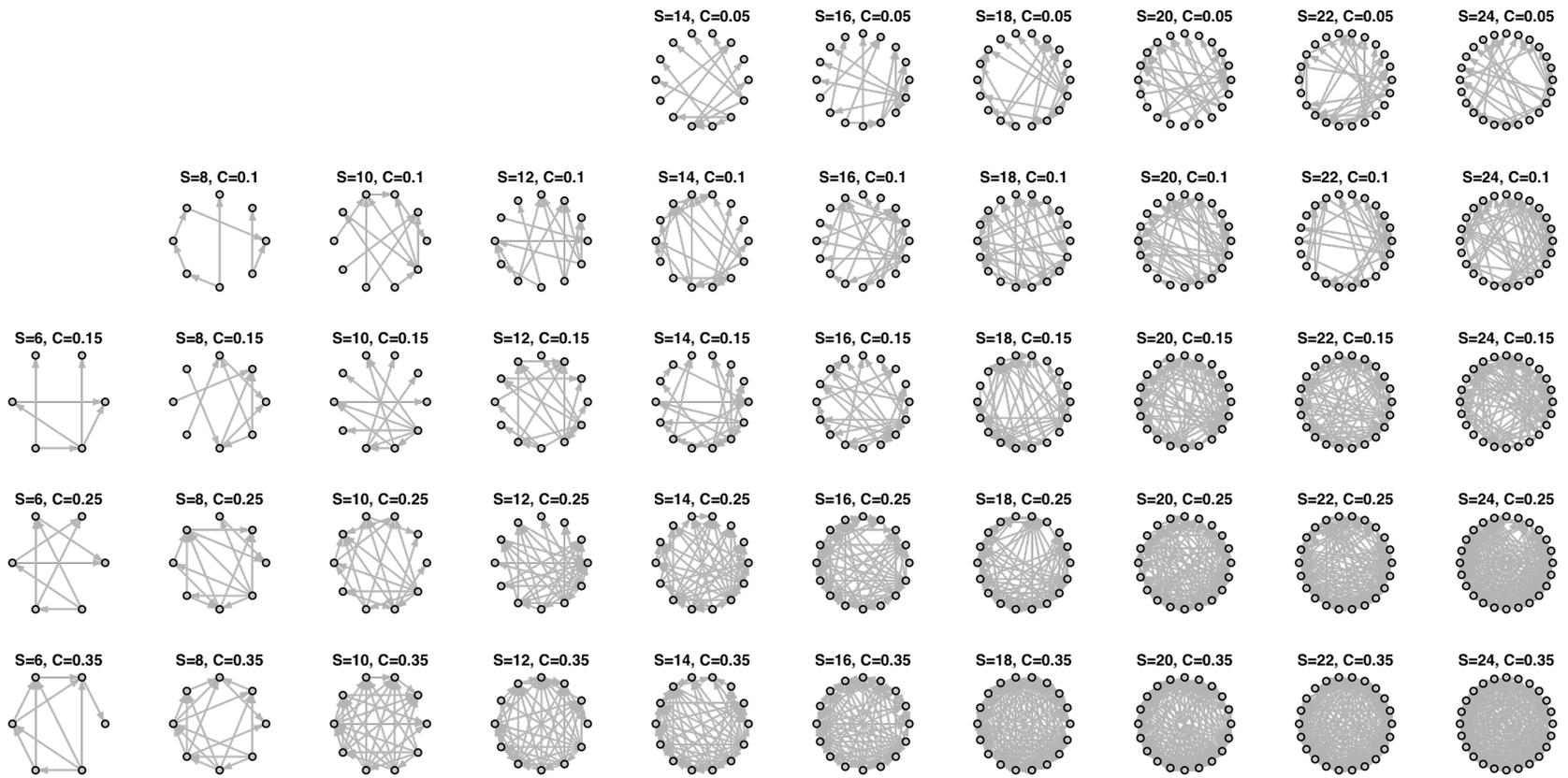


Figure B.9. Examples of the stochastic realizations of the niche model algorithm for each of the investigated species richness (S) and connectance level (C) combinations.

REFERENCES CITED

1. Dunne, J.A., R.J. Williams, and N.D. Martinez. (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, **5**(4): 558-567.
2. Dunne, J.A., R.J. Williams, and N.D. Martinez. (2004) Network structure and robustness of marine food webs. *Marine Ecology Progress Series*, **273**: 291-302.
3. Townsend, C.R., R.M. Thompson, A.R. McIntosh, C. Kilroy, E. Edwards, and M.R. Scarsbrook. (1998) Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters*, **1**(3): 200-209.
4. Huxham, M., S. Beaney, and D. Raffaelli. (1996) Do Parasites Reduce the Chances of Triangulation in a Real Food Web? *Oikos*, **76**(2): 284-300.
5. Hall, S.J. and D. Raffaelli. (1991) Food-Web Patterns: Lessons from a Species-Rich Web. *Journal of Animal Ecology*, **60**(3): 823-841.
6. Baird, D. and R.E. Ulanowicz. (1989) The Seasonal Dynamics of The Chesapeake Bay Ecosystem. *Ecological Monographs*, **59**(4): 329-364.
7. Memmott, J., N.D. Martinez, and J.E. Cohen. (2000) Predators, Parasitoids and Pathogens: Species Richness, Trophic Generality and Body Sizes in a Natural Food Web. *Journal of Animal Ecology*, **69**(1): 1-15.
8. Havens, K. (1992) Scale and Structure in Natural Food Webs. *Science*, **257**(5073): 1107-1109.
9. Yodzis, P. (1998) Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *J Anim Ecology*, **67**(4): 635-658.
10. Warren, P.H. (1989) Spatial and temporal variation in the structure of a freshwater food web. *Oikos*, **55**(3): 299-311.
11. Link, J. (2002) Does food web theory work for marine ecosystems? *Marine Ecology Progress Series*, **230**: 1-9.
12. Martinez, N.D., B.A. Hawkins, H.A. Dawah, and B.P. Feifarek. (1999) Effects of sampling effort on characterization of food-web structure. *Ecology*, **80**(3): 1044-1055.
13. Opitz, S. (1996) Trophic interactions in Caribbean coral reefs. *ICLARM Technical Report 43, Philippines*.
14. Goldwasser, L. and J. Roughgarden. (1993) Construction and analysis of a large Caribbean food web. *Ecology*, **74**(4): 1216-1233.
15. Martinez, N.D. (1991) Artifacts or Attributes? Effects of Resolution on the Little Rock Lake Food Web. *Ecological Monographs*, **61**(4): 367-392.
16. Waide, R. and W. Reagan, *The food web of a tropical rainforest*. 1996, University of Chicago Press: Chicago.
17. Christian, R.R. and J.J. Luczkovich. (1999) Organizing and understanding a winter's seagrass foodweb network through effective trophic levels. *Ecological Modelling*, **117**(1): 99-124.
18. Polis, G.A. (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist*, **138**(1): 123-155.

Appendix C. *Mathematica commands for calculating the weighted predictions matrix.*

Mathematica commands for computing the Adjoint (**adjA**), Absolute Feedback (**T**), and Weighted-predictions (**W**) matrices given a community matrix **A** are as follows:

```
(* Specify community matrix *)
A = {{-1, 1, 1, 1}, {-1, -1, 1, 1}, {-1, -1, -1, 1}, {-1, -1, -1, -1}}

(* Or, import community matrix from file in working directory *)
Directory[]
A=Import["A.csv"];
A//MatrixForm

(* Create functions to compute matrix minors and matrix permanent *)
SetAttributes[ZD, Listable]; ZD[x_, y_]:= If[y == 0, 1, x/y];
Minor[m_List?MatrixQ, {i_Integer, j_Integer}]:=Abs[Drop[Transpose[Drop[Transpose[A], {j}]], {i}]]
Permanent[m_List]:= With[{v = Array[x, Length[m]]},Coefficient[Times @@ (m.v), Times @@ v]]

(* Calculate adjoint, absolute feedback, and weighted-predictions matrices *)
n = Length[A];
adjA = Inverse[-A]*Det[-A];
adjA//MatrixForm
T = Outer[Permanent[Minor[Abs[A], {##}]] &, Sequence @@ Range /@ Dimensions[A], 1];
T//MatrixForm
W = N[ZD[Abs[adjA], T]];
W//MatrixForm
```