

Predicting community responses to perturbations in the face of imperfect knowledge and network complexity

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Abstract. How best to predict the effects of perturbations to ecological communities has been a long-standing goal for both applied and basic ecology. This quest has recently been revived by new empirical data, new analysis methods, and increased computing speed, with the promise that ecologically important insights may be obtainable from a limited knowledge of community interactions. We use empirically based and simulated networks of varying size and connectance to assess two limitations to predicting perturbation responses in multispecies communities: (1) the inaccuracy by which species interaction strengths are empirically quantified and (2) the indeterminacy of species responses due to indirect effects associated with network size and structure. We find that even modest levels of species richness and connectance (~25 pairwise interactions) impose high requirements for interaction strength estimates because system indeterminacy rapidly overwhelms predictive insights. Nevertheless, even poorly estimated interaction strengths provide greater average predictive certainty than an approach that uses only the sign of each interaction. Our simulations provide guidance in dealing with the trade-offs involved in maximizing the utility of network approaches for predicting dynamics in multispecies communities.

Key words: community matrix; disturbance; ecosystem-based management; interaction strengths; loop analysis; observation error; prediction uncertainty; press experiments.

INTRODUCTION

A long standing, important, but still poorly solved problem in ecology is how best to predict the responses of species subjected to natural and anthropogenic disturbances. Natural communities are simply too species rich for all aspects of their complexity to be completely known. Consequently, virtually all efforts to understand community dynamics rely on simplifying assumptions, either formal or informal. These assumptions range from what types of interactions are most fundamental (e.g., trophic, competitive, mutualistic), to what species have the greatest impact (e.g., keystones, dominants), to what features of their interactions are

most critical in driving specific responses (e.g., distributions, interaction strengths, nonlinearities). All approaches seek to distill the complexity of nature down to manageable and measurable levels that nonetheless allow reliable predictions of system behaviors to be made.

The central feature of these efforts is the notion that all ecological communities are composed of species connected to each other both directly and indirectly through the shared network of direct species interactions. The presence of indirect effects means that species need not interact directly to affect each other's populations, and that direct effects may be counteracted by indirect effects. For example, in an intraguild predation scenario (Fig. 1), the net effect of the intermediate consumer (B) on the top consumer (A) arises from both its positive direct effect as a source of

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food, but also a negative indirect effect caused by exploitative competition for their shared resource (C). Insights into the structure of community interaction networks have thus been fundamental to our understanding of the factors that organize communities and affect their dynamics through the propagation of perturbations (Wootton 1994, Polis and Winemiller 1996, Bascompte 2009). Accordingly, calls for more highly resolved empirical networks and the quantification of their interaction strengths are pervasive in the ecological literature (e.g., Borer et al. 2002, Cohen et al. 2003). The application of network approaches has also become important in applied ecology, where holistic, ecosystem-based approaches to the management of multispecies communities are increasingly advocated. Consideration of interaction networks and their indirect effects is becoming common in fisheries management, pest control, and conservation science (e.g., Ramsey and Veltman 2005, Macfadyen et al. 2009, Worm et al. 2009).

The complexity of species interaction networks itself nevertheless poses several major obstacles for the prediction of community effects following even simple perturbations. Primary among these are the difficulty of quantifying the strengths of species interactions, and the manner by which loops of reticulate interaction chains can magnify or dampen the effect of each direct interaction (Fig. 1). While these problems are generally appreciated, it is not yet clear how severely they limit our ability to understand community dynamics, especially given the limited information upon which community-wide analyses are virtually always based. Yodzis (1988a, b) was among the first to quantify the dramatic effects that the misspecification of interaction strengths can have for predictions of community dynamics, showing that order-of-magnitude errors in the estimation of interaction strengths could routinely reverse the direction by which species abundances are predicted to respond to a perturbation elsewhere in the food web (see also Montoya et al. 2009). Indirect effects and variation in interaction strengths can combine to affect positive species responses even in systems of pure competition where each species' direct effect on another is negative (Stone and Roberts 1991, Roberts and Stone 2004). Others have highlighted how much of this directional indeterminacy is affected by network topology alone, independent of variation in interaction strengths (Dam-bacher et al. 2002, 2003a).

A systematic understanding of when topology and imprecise interaction strength estimates will combine to limit predictive success is essential in the careful and robust application of network approaches. We therefore revisit Yodzis (1988a, b) and use empirically based and model food webs of varying size and complexity to systematically ascertain how precisely the strengths of species interactions must be estimated to accurately predict the directional response of species abundances to perturbations. Interaction strengths are now commonly

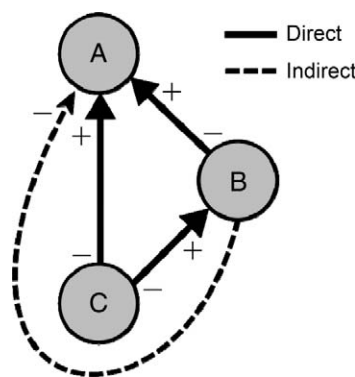


FIG. 1. The potential for indirect effects and the misestimation of direct interaction strengths to combine and reverse the predicted response of a species to perturbations elsewhere in the community is evident even in networks of low complexity. In an intraguild predation system, a perturbation that increases the abundance of the intermediate consumer (B) could affect either an increase (+), a decrease (-), or no change in the abundance of the omnivore (A) if the strength of their direct interaction were to be respectively estimated to be greater, less than, or precisely equal to the magnitude of their indirect interaction as mediated by their shared basal resource (C).

estimated by a variety of approaches (Wootton and Emmerson 2005, Novak and Wootton 2010), but the predictive potential of these or qualitative approaches in species-rich systems remains largely unknown.

We make use of the community matrix (Levins 1968) as a means of encapsulating the strength and topology of all the pairwise direct interactions in a network. Indirect effects such as trophic cascades are emergent consequences of these direct interactions, mediated solely by changes in species abundances. Our analyses focus on predicting the long-term effects of small press perturbations on species abundances and thereby differs from other analyses assessing the effects of complete species removals (e.g., Dunne et al. 2002). Press perturbations (the systematic change to any parameter affecting a population's growth rate, as in the continuous removal or addition of individuals) are representative of many of the disturbances that communities experience, such as the effects of fisheries harvest, pollution, eutrophication, or a controlled experiment (Bender et al. 1984, Yodzis 1995). Application of theoretical press perturbations to the community matrix reveal the net effects of such disturbances on equilibrium species abundances, as shifts in abundances propagate through a community via all its direct and indirect interactions. The power of this approach is that it stipulates each species' dynamics only as

$$\frac{dN_i}{dt} = f_i(N_1, N_2, \dots, N_S) \quad i = 1, \dots, S$$

where the function f_i could represent any conceivable relationship between the abundance (N) of species i and all other S species (Yodzis 1981, 1988a, 1995). Each ij element of the community matrix represents the partial

derivative of f_i with respect to the abundance of species j (i.e., $\mathbf{A}_{ij} = \partial f_i / \partial N_j$), reflecting the direct effect of a small change in species j 's abundance on species i 's growth rate. The underlying structural conjecture is thus that each species' dynamics can in fact be described by some continuous function. Species interactions and dynamics need not themselves be linear, but rather are assumed to be well-represented by a linearization near equilibrium abundances (Stone and Roberts 1991, Haydon 1994). Our analyses therefore provide a first-order rendition of other more detailed, restrictive, and data-hungry modeling efforts.

Our findings caution against placing too much weight on predictions from networks with more than ~ 25 pairwise interactions in the absence of exceptionally accurate empirical data. However, we also show that even comparatively poorly quantified interaction strengths offer more predictive reliability on average than does a qualitative approach that specifies only network topology and the sign of each interaction. Further analyses investigating the effects of network size and complexity on the prevalence of topological indeterminacy offer guidance in the application of network approaches in community ecology by quantifying the limits of their predictive reliability. We conclude by discussing alternative strategies to maximize the utility of network approaches for predicting dynamics in species-rich communities.

MATERIALS AND METHODS

Prediction error in empirical food webs

We first conducted a set of analyses based upon 17 empirical food webs whose topologies are considered to be among the most well-characterized of any interaction networks available (Appendix B: Table B1; see Dunne et al. 2002, 2004), although the strengths of their species interactions are unknown. We studied both the aggregated and original versions of these networks. The aggregation of taxa with shared sets of predators and prey reduced the structural biases associated with their reconstruction (Williams and Martinez 2000), avoided degenerate community matrices in qualitative modeling (Appendix A), and remained representative of the network topologies of nature. In typical fashion we converted each network to a quantitatively specified community matrix (henceforth denoted by ${}^{\#}\mathbf{A}$, following Dambacher et al. [2003a]) as follows: The diagonal elements specifying self-limitation terms of all basal species, ${}^b\alpha_{ii}$, were set to -1 (May 1972), while the ${}^c\alpha_{ii}$ terms of consumer species were set to $1/1000$ th of that of the basal species (Yodzis 1988b). (Henceforth, superscripts b and c respectively refer to basal and consumer species.) By specifying negative diagonal elements we effectively assumed that all species interactions were non-saturating (type I- or type III-like functional responses) and that population sizes were at a feasible equilibrium (Haydon 1994). Off-diagonal negative top-down interaction strengths of consumers on their prey,

α_{ij} , were drawn from a beta distribution (Beta[1,4]) to reflect the skewed nature of empirical interaction strength distributions (Wootton and Emmerson 2005). This distribution was truncated such that the effects of consumer j on resource i were constrained to lie within the limits ${}^c\alpha_{ii} > \alpha_{ij} > {}^b\alpha_{ii}$. Positive bottom-up interaction strengths were specified as $\alpha_{ji} = -e\alpha_{ij}$, with conversion efficiency e set to 0.1 for all interactions. This process of converting the empirical webs to matrix form introduced the unavoidable result that only one of any two reciprocal predators was deemed to feed upon the other. We specified directionality to this fraction of interactions at random (see also Allesina and Pascual 2008).

The negative of each ${}^{\#}\mathbf{A}$ was inverted to predict the response of species to press perturbations in their food web (Bender et al. 1984, Yodzis 1988b). Each element of $-{}^{\#}\mathbf{A}^{-1}$ reflects the direction and relative (within-column) magnitude by which the local equilibrium abundance of a species in row i (N_i^*) will respond to a sustained small input of individuals to the species in column j (I_j) because

$$-({}^{\#}\mathbf{A}^{-1})_{ij} = \frac{\partial N_i^*}{\partial I_j}$$

obtained using the differentiation of $f_i(N_1, N_2, \dots) = 0$ for all $i \neq j$ and $f_j(N_1, N_2, \dots) + I_j = 0$ with respect to I_j (Bender et al. 1984, Yodzis 1988b). That is, since $\partial N_i^* = -({}^{\#}\mathbf{A}^{-1})_{ij} \times \partial I_j$, a small press perturbation I_j will cause a change in species i 's equilibrium abundance that is proportional to $-({}^{\#}\mathbf{A}^{-1})_{ij}$. The net effects expressed by the ij th element of $-{}^{\#}\mathbf{A}^{-1}$ occur via all the direct and indirect chains of interactions linking the two species (Yodzis 1988b). The diagonal elements of $-{}^{\#}\mathbf{A}^{-1}$ reflect the net result of each species' own indirect effects on itself as mediated by the other species in the network (Haydon 1994). We used the resulting sign-structure of each $-{}^{\#}\mathbf{A}^{-1}$ to specify each network's set of "true" directional responses (i.e., predictions with no estimation error).

Error in interaction strength estimates was then added to each interaction value of ${}^{\#}\mathbf{A}$. For each non-zero α_{ij} we randomly chose (with equal probability) to draw a new value either from a $[\alpha_{ij}, \alpha_{ij} \times F]$ uniform distribution, representing an overestimate of the true α_{ij} , or from a $[\alpha_{ij}/F, \alpha_{ij}]$ uniform distribution, representing an underestimate of the α_{ij} , where parameter F specified the maximum possible proportional error of an estimate (Yodzis 1988b). This ensured that (1) no directional bias in misestimation occurred, and that (2) the maximum possible error was proportional to the magnitude of the expected interaction strength itself, as is likely to be the case for empirical estimates (Novak and Wootton 2008). F was varied systematically between 1 (no error) and 10 (an order of magnitude error, as in Yodzis 1988b) while ensuring $\alpha_{ij} < {}^c\alpha_{ii}$ for all species. To assess the effects that this estimation error had on predictive accuracy we calculated the proportion of elements in $-{}^{\#}\mathbf{A}^{-1}$ without introduced error that matched the sign-structure of the

respective elements in $-\#A^{-1}$ with introduced error at each F error level for each empirical network. The process of specifying “true” interaction strengths, adding increasing amounts of estimation error, and assessing predictive accuracy was repeated once for each of 100 realizations of A for each empirical network.

To assess the sensitivity of our results to chosen interaction strength parameters, we repeated our analyses with (1) e set to either 0.5 or 0.9, (2) interactions specified to an order of magnitude greater strength ($\alpha_{ij} > {}^b\alpha_{ij} = -10$), and (3) by drawing α_{ij} from uniform (Beta[1, 1]) or more strongly skewed (Beta[1, 6]) distributions. To assess the utility of focusing future empirical efforts on measuring only a subset of the interactions in a community we repeated the analyses allowing either the strength of (1) only the strongest or (2) only the weakest interactions to be estimated with error (i.e., the upper or lower 50th quartile of α_{ij} values, respectively). We also assessed the degree to which the species-specific linkage densities of a network (the proportion of species in a network connected to only one or two other species) could be used to explain predictive success.

We next investigated the reliability of predictions of species responses when interaction strengths are entirely unknown and only the structure and qualitative sign of each non-zero interaction of a network is specified (Mason 1953, Levins 1968). Each aggregated network's $\#A$ was converted to qualitatively specified form (henceforth denoted by ${}^\circ A$ following Dambacher et al. 2002) by removing information on the magnitude of α_{ij} elements. We then used the matrix methods of loop analysis to predict directional species responses by calculating the matrix adjoint, $\text{adj}(-{}^\circ A) = -{}^\circ A^{-1} / \det(-{}^\circ A)$ (Dambacher 2002; Appendix A) and determined the proportion of elements in $\text{adj}(-{}^\circ A)$ that matched the sign-structure of the respective elements in $-\#A^{-1}$ without error.

Prediction error in model food webs

We used the niche model algorithm of Williams and Martinez (2000) to tease apart the effects of network size and complexity inherent in our use of the empirical networks. This algorithm, which has seen broad validation as a way to generate “realistic” networks by a variety of metrics measured in empirical food webs (e.g., Williams and Martinez 2000, Dunne et al. 2004, Stouffer et al. 2006), allowed us to create replicate food webs of systematically varying species richness and connectance. Requiring the specification of species richness (S) and connectance (C_d , the proportion of possible interactions that is realized as L links, L/S^2), the algorithm begins by assigning each species to a random position on a one-dimensional niche axis (n_i drawn from a $\text{Unif}[0, 1]$). Each species' diet breadth along this axis is stochastically specified, with its potential diet range, r_i , and diet center, c_i , defined as $r_i = n_i \times x_i$, where $x_i \sim \text{Beta}[1, 1 - 1/(2C_d)]$ and $c_i \sim \text{Unif}[r_i/2, n_i]$ (Bagdassarian et al. 2007). Species i feeds on all species within its

feeding range, but the species with the smallest n_i does not prey on any other species (Williams and Martinez 2004).

We created food webs of 6 to 100 species at five possible connectance levels ($C_d = (0.05, 0.1, 0.15, 0.25, 0.35) \pm 0.02$) reflecting the range of richness and connectance levels observed in the empirical networks (Table B1). These were converted into community matrix form if all species were connected in a single network. We then repeated our assessment of quantitative interaction strength estimation error ($-\#A^{-1}$ vs. $-\#A_{\text{error}}^{-1}$) and loop analysis ($-\#A^{-1}$ vs. $\text{adj}(-{}^\circ A)$) as above, calculating the proportion of qualitative matches across 100 replicate networks having positive determinants at each richness-connectance level.

Limits to structural predictive reliability

If quantitative and qualitative analyses of food web perturbations may frequently be inaccurate, one would like to know which networks will have this limitation and which will not. To approach this issue we used the weighted-predictions matrix (W) of loop analysis to further investigate how network size and complexity contribute to variation in predictive reliability associated with network structure itself (Dambacher et al. 2002, 2003a). Each element of W reflects the ratio of the net effects (positive or negative) of a species in column j on the species in row i and the total number of feedback loops that link the two species in ${}^\circ A$ (Appendix A). A w_{ij} value of 0 thereby indicates that half of the feedbacks linking two species have net positive structural effect and the other half have net negative effect (a 1:1 ratio); a value of 0.5 reflects a ratio of 3:1. Species pairs with low w_{ij} are expected to have low structurally predictive reliability, their net effects being more dependent upon the strengths of their direct and indirect interactions, while pairs with high w_{ij} are expected to have reliably predictable net effects. Dambacher et al. (2002) suggest a confidence cut-off level of 0.5 for the assignment of structurally reliable predictions because predictions with $w_{ij} > 0.5$ exhibit high sign determinacy; predictions having $w_{ij} > 0.5$ were associated with consistent predictions >90% of the time in simulations (Dambacher et al. 2003a, Hosack et al. 2008). Note that high structural reliability need not necessarily indicate prediction correctness.

We used the niche model to create food webs of 6–24 species at connectance levels of 0.05–0.35. Prior applications of the weighted-predictions matrix have been restricted to networks of ≤ 10 species (Dambacher et al. 2002, 2003a, b, Hosack et al. 2008). Self-limitation was imposed on all species by setting diagonal elements to -1 (Dambacher et al. 2002, 2003a). A potential network was rejected when $\det(-{}^\circ A) > 0$ so that all accepted networks could be inverted. For each of five networks produced at each possible richness-connectance combination we used Mathematica (Wolfram Research, Inc, Champaign, Illinois, USA) to calculate

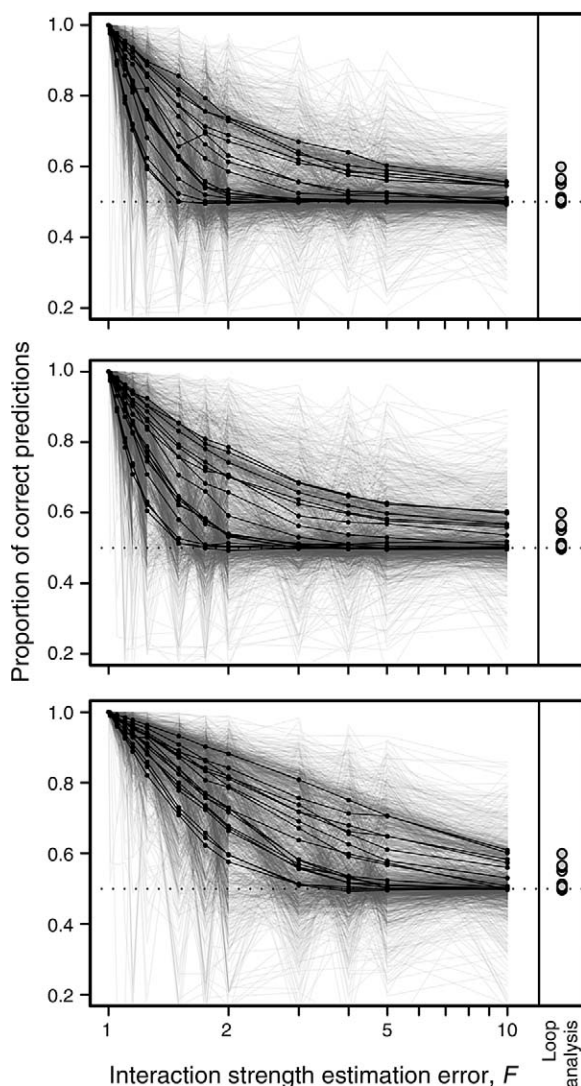


FIG. 2. The proportion of qualitatively correct species response predictions declines as a function of the error by which interspecific interaction strengths are estimated in 17 well-characterized empirical food webs. The mean for each network is in black; $n = 100$ individual true- α_{ij} realizations for each network are in gray. A proportion of 0.5 corresponds to predictive success matching that of flipping a coin. The figure illustrates the rate of decline observed when: (a) all interactions are estimated with equal likelihood of error; (b) only the weakest interactions are estimated without error; and (c) only the strongest interactions are estimated without error. 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 (a) all, (b) the strongest, or (c) the weakest interactions. The proportion of correct predictions made for each network by loop analysis, which uses network topology alone assuming no knowledge of interaction strengths, is also shown (see *Methods: Prediction error in empirical food webs*). Note the log scale of the x-axis.

W (Appendix C). We calculated the mean and 95th percentile of weighted predictions within each **W**, and tallied the number of predictions having $w_{ij} > 0.5$ to assess how predictive reliability varied with network

size, connectance, and the total number of predator–prey interactions.

RESULTS

The accuracy of interaction strength estimates

Increasing amounts of introduced error in interaction strength estimates led to a decreasing proportion of correctly made predictions in all empirical food webs (Fig. 2). In some networks (e.g., Little Rock lake and Caribbean Reef) the mean proportion of correctly made predictions dropped to 50% (equivalent to predicting a species' response by flipping a coin) when interactions were not estimated to within $\pm 100\%$ of their true value (proportional error $F < 2$, Fig. 2a). Other networks (e.g., Canton Creek and Ythan Estuary) exhibited an average of $>75\%$ correct predictions at this level of estimation accuracy. These networks retained better-than-random mean predictive success even when interaction strengths were estimated to within only an order of magnitude of their true value ($F = 10$). With one exception (Bridge Brook lake) our use of aggregated rather than non-aggregated versions of the empirical networks had either little effect on these results or increased mean predictive success by up to 9.5% at intermediate levels of estimation error (Appendix B: Fig. B5). With increasing estimation error the mean proportion of correctly made predictions tended to converge on the predictive success of loop analysis ($r^2 = 0.95$, $t = 12.3$, $P < 0.001$ at $F = 10$, Appendix B: Fig. B1). Variation in predictive success was large however, with many individual quantitative realizations performing worse than their qualitative counterpart. Mean predictive success at an order-of-magnitude error was positively but weakly correlated with the proportion of species in a network that were linked to only one or two other species ($r^2 = 0.46$, $t = 1.98$, $P = 0.07$). The 95th quantile of correctly made predictions at $F = 10$, on the other hand, was positively and strongly correlated with the proportion of species in a network that were linked to only one or two other species ($r^2 = 0.93$, $t = 10.20$, $P < 0.0001$; Appendix B: Fig. B4).

Relative to the situation where all interactions were measured with error, the rate by which mean predictive accuracy declined with increasing error was little affected when only weak interactions were measured accurately (Fig. 2b), but was reduced when strong interactions were estimated accurately (Fig. 2c). However, at high F values, even these simulations, with all strong interaction estimated without error, illustrated extremely poor predictive success (Fig. 2c). Alternate conversion efficiencies, maximum interaction strengths, and interaction strength distributions generally had negligible effect on these patterns, although conversion efficiencies of $e = 0.9$ tended to reduce the rate by which predictive accuracy declined as estimation error increased (Appendix B: Fig. B6).

We found the same general result in simulations of niche model networks: falling accuracy in interaction

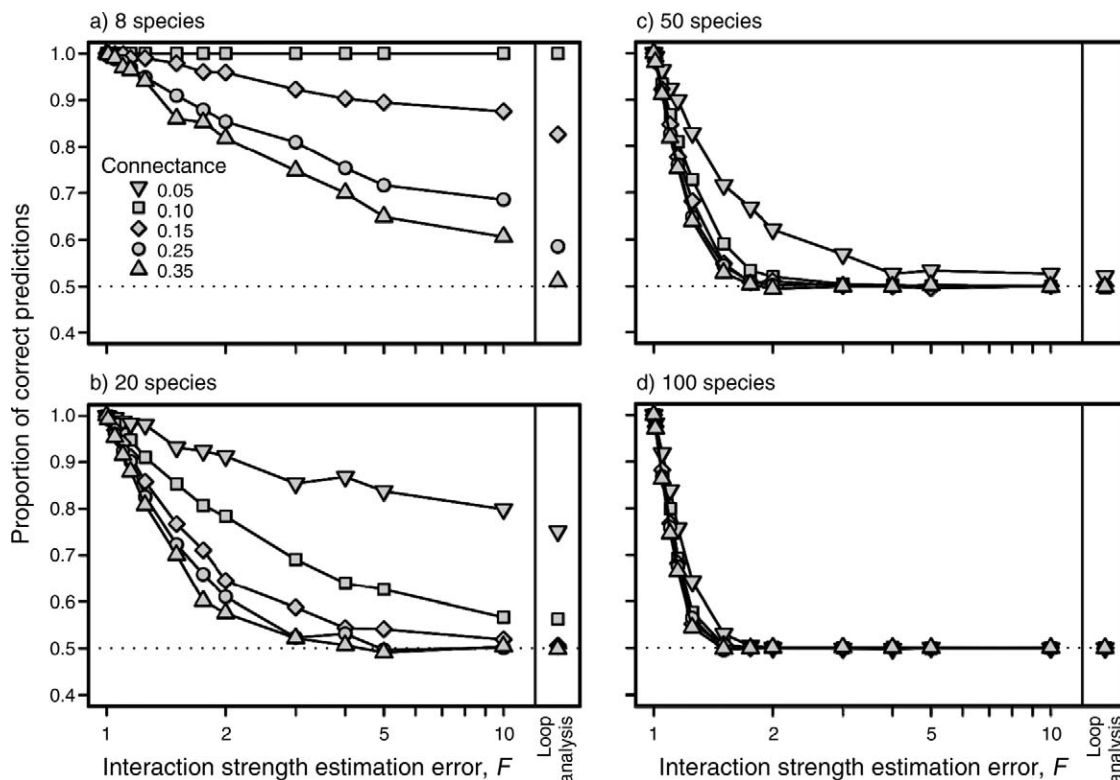


FIG. 3. The mean proportion of qualitatively correct species response predictions declines as a function of the error (F) by which interspecific interaction strengths are estimated in niche model networks of varying size and complexity. Loop analysis uses network topology alone, assuming no knowledge of interaction strengths. See *Methods: Prediction error in empirical food webs* and Fig. 2 for details. Only networks of (a) species richness $S = 8$, (b) 20, (c) 50, and (d) 100 species are shown; others are shown in Appendix B: Fig. B7. Connectance reflects directed connectance.

strength estimates decreased the mean proportion of correctly made predictions (Fig. 3). As with the empirical networks, the mean proportion of correct predictions made with quantified interaction strengths tended to converge on the proportion of correct predictions made by loop analysis as estimation error increased ($r^2 = 0.95$ at $F = 10$; Appendix B: Fig. B2). Predictions were fully indeterminate (50% predictive success) in all networks of 100 species when interaction strengths were not estimated to within $\pm 100\%$ of their true value ($F < 2$) regardless of connectance level (Fig. 3d). In networks of 20 species the proportion of correct predictions approached 50% when interaction strengths were estimated with $F > 4$ when $C_d > 0.15$, but remained above 80% when $C_d = 0.05$ even when interactions were estimated to within an order-of-magnitude accuracy ($F = 10$, Fig. 3b). Networks of 8 species and $C_d = 0.1$ retained 100% correct predictions regardless of estimation error. This occurred because they consisted of either a simple linear interaction chain or a non-reticulate tree structure (Appendix B: Fig. B9).

Limits to qualitative reliability scores

The mean and 95th percentile of weighted predictions values, as well as the proportion of predictions deemed

reliable (i.e., $w_{ij} > 0.5$), diminished rapidly as network size and connectance increased (Fig. 4a–c). On average, no structural reliability score exceeded 0.5 in networks of 24 species regardless of their connectance. Only in networks of low connectance ($C_d \leq 0.15$) was the average proportion of structurally reliable predictions likely to exceed 20% in networks of 10 or more species. A good predictor for the proportion of predictions having $w_{ij} > 0.5$ was the total number of predator–prey interactions present in the network (Fig. 4d). Only 1.5% of all networks with more than 25 links had more than 1% of their predictions associated with w_{ij} values greater than 0.5. All networks with more than 35 links had less than 1% structurally reliable predictions.

DISCUSSION

The pessimist's view

Natural communities typically contain hundreds to thousands of species with the potential of interacting with one another in a vast number of ways (Polis and Strong 1996; see Plate 1). Our findings therefore suggest a daunting scenario for predicting the response of species to perturbations elsewhere in their community. Using simplified descriptions of nature's true complexity that focused only on trophic interactions, our analyses

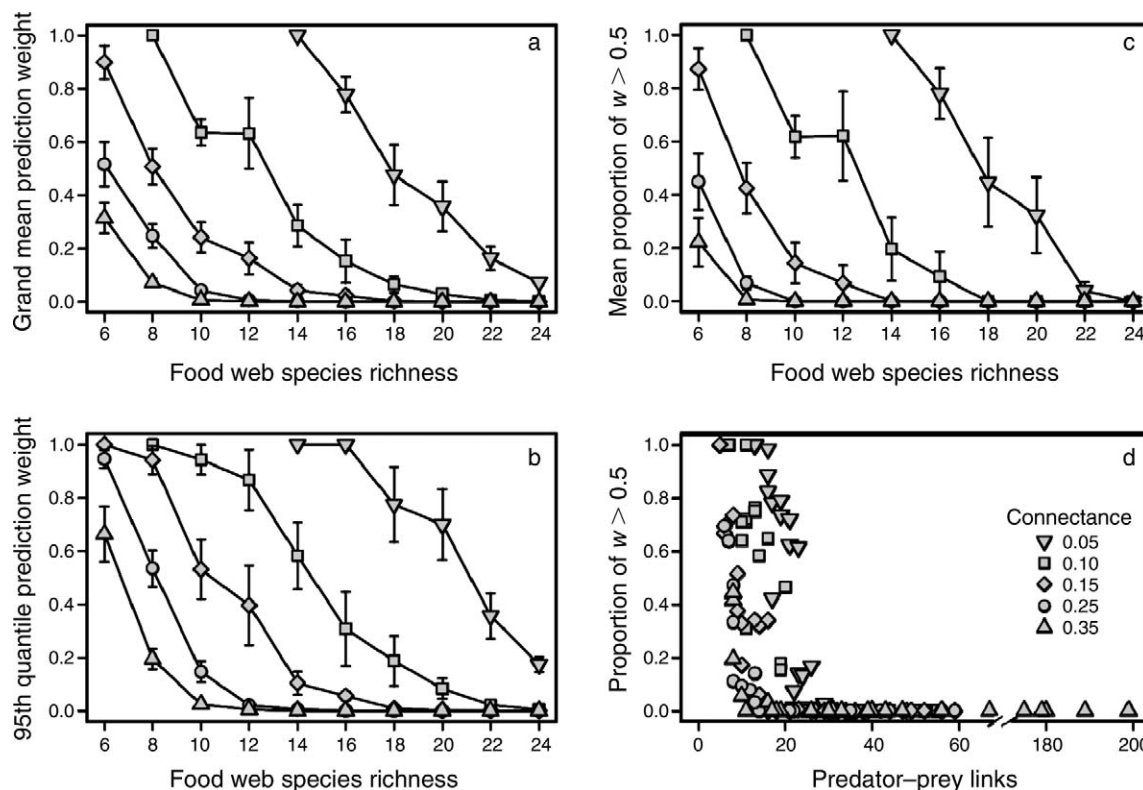


FIG. 4. Predictive insight into the structural indeterminacy of a network as measured by (a) the grand mean of weighted-predictions (w_{ij}), (b) the mean 95th quantile of w_{ij} , and (c) the proportion of predictions deemed reliable ($w_{ij} > 0.5$) decreases rapidly with increasing network size and connectance (\pm SE). (d) The proportion of structurally reliable predictions declines to zero as the number of interspecific links in a network exceeds ~ 25 . See *Methods: Limits to structural predictive reliability* and Appendix A for details. Note the break in the x-axis. Connectance reflects directed connectance.

of empirical and model network structures demonstrate the accuracy that is needed in estimating species interaction strengths to avoid erroneous predictions due to indirect effects. Our ability to predict the response of a species to a perturbation elsewhere in its network declined to the level of flipping a coin in most empirical networks, and in model networks of ≥ 50 species, when interaction strengths were not measured to within 100% of their true value (Figs. 1 and 2). As estimation errors were assumed to follow uniform distributions in our simulations, the ardent pessimist might even argue that average estimates need be twice as accurate still. Seeking to predict only the direction, not the magnitude, of a species' response, our simulations assumed non-saturating interactions and no interaction modifications, prey switching, or spatiotemporal variation in interaction strengths, all of which occur in nature (Doak et al. 2008). Therefore, observation error and structural indeterminacy due to indirect effects alone set the limits of predictive success in networks of moderate to large size or complexity. Our use of aggregated rather than non-aggregated versions of the empirical networks further simplified their true complexity of species-specific differences. The niche model networks that teased apart the effects of size and complexity suggest

extremely limited predictive reliability in realistically connected networks of more than 24 species, or more generally in networks exhibiting more than ~ 25 pairwise species-to-species interactions (Fig. 4). Even more discouragingly, simulations that assumed perfect knowledge of all strong interaction still yielded poor predictive power if weak interactions were not reasonably well characterized (Fig. 2). This implies that multiple weak interactions have the power to strongly shape community-wide responses to perturbations. Given the generalized assumptions of our analyses these conclusions are expected to hold for alternative predictive approaches having more specific model formulations (e.g., Ecopath, allometric models [see Yodzis 1981, 1988a, 1995]).

The optimist's view

The good news is that there are numerous counter-arguments to this discouraging interpretation of our results. For one, our approach assumed that all post-perturbation dynamics have played-out such that each species has reached a new point equilibrium abundance. Even in an empirical reality where perturbations are more variable and equilibrium conditions may never be attained, it may be easier to predict short-term, transient responses. Methods for unraveling the temporal prop-

agation of indirect effects between a system's equilibria (Yodzis 1988b, 1995, Higashi and Nakajima 1995, Takimoto et al. 2009) or in systems of bounded non-equilibrium dynamics (Puccia and Levins 1985, Damacher et al. 2009) are available. In theory certainly, first-order impacts are completely predictable, depending only on the sign and strength of the interactions between the perturbed species and its directly linked neighbors (Yodzis 1995). How quickly this predictability declines empirically will be a function of the timescales over which species abundances respond to propagate the perturbation. Empirical studies suggest that such propagation can occur rapidly (Menge 1997).

An important empirical question emerging from our analyses concerns the accuracy by which interaction strengths can in fact be estimated. This is an essential issue because interaction strengths among species pairs vary considerably in real food webs (Wootton and Emmerson 2005). Notwithstanding spatiotemporal process variation, is a level of accuracy to within 100% ($F = 2$) easily obtained or clearly out of reach for most empirical systems? Very few studies have explicitly compared independent interaction strength estimates in natural contexts. The predictions of some interaction strength estimates have shown remarkable correspondence to independent experimental effects (e.g., Wootton 1997, O'Gorman et al. 2010). A recent study directly comparing per capita interaction strengths derived from manipulative experiments to those of an observational approach yielded estimates that differed from as little as 5% up to 610% (Novak 2010). These differences are certainly better than an order-of-magnitude error ($F = 10$; Yodzis 1988b). Further efforts to quantify estimation accuracy, and to distinguish process from observation error (Hilborn and Mangel 1997, Wootton and Emmerson 2005), would help place the results of our simulations in context.

Further hope is offered from our analyses by (1) the variation in the mean predictive success observed between different empirical networks and (2) by the variation around the mean predictive success observed across replicate realizations of each empirical network. That is, while the mean predictive success of some networks dropped to 50% quite rapidly with increasing estimation error, and a large fraction of individual realizations exhibited worse-than-random predictive success with only 1% estimation error for some networks, the converse was also true: Some networks (e.g., Canton Creek, Ythan Estuary, Scotch Broom, and Chesapeake Bay) retained better-than-random predictive success even when interaction strengths were entirely unknown (Fig. 2; Table B1). In other networks (e.g., Grassland) individual realizations exhibited up to 80% predictive success, even when mean success across all realizations was only 50% at an order-of-magnitude estimation error (Appendix B: Fig. B3). These observations, and the fact that the 95th quantile (rather than the mean) of predictive success at an order-of-magnitude

error was tightly correlated with the proportion of poorly connected species in a network (Appendix B: Fig. B4), indicate that certain network topologies, species in key topological positions, or the strengths of some key interactions, are more important for preserving predictive success than are others (see also Montoya et al. 2009). The analyses presented here cannot distinguish whether these key positions or key interactions directly correspond to poorly connected species; other species (or interactions), including richly connected species, could produce the same results if they are themselves linked directly to (or directly link) the poorly connected species. Further analyses are needed to discriminate between these nonexclusive alternatives to determine the degree to which particular species characteristics can be attributed the cause of predictive success. Since mean predictive success at an order-of-magnitude error was little affected in simulations where all weak (Fig. 2b) or all strong (Fig. 2c) interactions were estimated with full accuracy, the answer is not as simple as distinguishing among species pairs with strong vs. weak interactions. Similarly, since networks that exhibited equally poor predictive success using loop analysis differed in their mean predictive success at better-than order-of-magnitude levels of estimation error, the answer does not lie with network topology alone. The potential body-size mediated association between the strengths of a species' interactions and its structural position in a network may offer empirical focus to these observations (O'Gorman et al. 2010); our simulations specified the position of strong and weak interactions at random.

The way forward

The observation that the mean predictive success of the quantified interaction strength approach converges to the predictive success of loop analysis as estimation accuracy declines suggests that having some knowledge of interaction strengths will, on average, be better than having none at all (Figs. 1 and 2). Furthermore, the accurate estimation of strong interactions reduces the rate at which mean predictive success declines with increasing estimation error (Fig. 2c). A better understanding of the empirical species-pair attributes associated with strong interactions may therefore provide a means to focus empirical efforts to increase predictive success. Accumulating empirical evidence suggests that such attributes may include the ratio of predator to prey body sizes and metabolic rates (Wootton and Emmerson 2005, Brose et al. 2008). Furthermore, strong interactions are likely to be measured more accurately than weak interactions (Novak and Wootton 2008). Nonetheless, an exclusive focus on strong interactions is ill-advised: the accurate estimation of strong interactions provided no increase in predictive success when weak interactions were estimated to within an order-of-magnitude error (Fig. 2). The importance of quantifying both strong and weak interactions extends to efforts



PLATE 1. Analyses of empirical and simulated interaction networks suggest that species interactions must be accurately estimated to reliably predict the response of species to perturbations elsewhere in their community, even when communities are relatively species-poor. This small ($<0.125 \text{ m}^2$) area of the Oregon (USA) intertidal contains at least 30 species visible to the naked eye of the >300 species that occur in this habitat. Photo credit: R. T. Novak.

assessing the stability of ecological communities (O'Gorman and Emmerson 2009).

Other than focusing on the poorly connected species of a network and increasing the accuracy by which we measure interaction strengths, what else can we do to increase predictive success? Our investigation of how network size and complexity contribute to the decline of predictive reliability suggest that indirect effects set the limits in realistically connected networks of more than 24 species (Fig. 4a, b). Networks with more than ~ 25 links retained extremely limited predictive reliability associated with their structure alone (Fig. 4c). For networks of pure competition communities such dependence of net effects on the number of links rather than species per se has been shown analytically (Roberts and Stone 2004) and could be used to guide empirical effort. Our analyses suggest that the further aggregation of species into trophic groups beyond their mutually identical predator and prey associations is unlikely to be fruitful; the resultant increase in connectance can quickly offset its benefits (Fig. 4). An extensive literature on species aggregation raises additional concerns (Yodzis and Winemiller 1999), including its effects on the misestimation of interaction strengths (e.g., Gardner et al. 1982, Bender et al. 1984, Fulton et al. 2003).

An alternative approach might consider only groups of <24 species at a time, particularly when these are organized into network compartments (e.g., Krause et al. 2003, Allesina and Pascual 2009). When present, compartments should limit the propagation of indirect

effects to reduce indeterminacy, just as they are thought to increase network stability (May 1972, Krause et al. 2003). In theory, species receiving or affecting only very weak interactions, or responding on very different timescales due to differences in generation times, might be safely ignored when predicting post-perturbation population sizes (Schaffer 1981, Bender et al. 1984). The same should extend to network compartments. Efforts to predict species responses to perturbations might thereby be simplified by hierarchical analyses of the less connected sub-networks. The efficacy of this approach will depend on the strength of compartmentalization (the relative number of links between vs. within compartments) and the extent to which interactions between compartments are weak. More work is needed to assess the degree to which species attributes such as body size, phylogeny, or habitat associations are associated with objective measures of group membership (Allesina and Pascual 2009).

An additional means to reduce predictive uncertainty holds further promise. Where available, prior information on how a subset of species responds to known perturbations elsewhere in their community could be used to constrain the universe of perturbation responses expected in other species. For the networks of our simulations such information was unavailable. Predictive certainty should increase as the ratio of prior information to network size and complexity increases. The fusion of loop analysis and Bayesian belief networks by Hosack et al. (2008) provides a powerful means of

incorporating such knowledge in the context of explicit network structures and offers an exciting direction for further development.

CONCLUSIONS

Predicting the response of species to perturbations in their community will remain a difficult endeavor in all but the simplest and most well-defined ecological systems. It seems prudent to restrict the predictive application of qualitative methods to abstracted networks and to communities typically dealt with in logistically tractable experiments; the power of loop analysis lies in the analysis of a network's indeterminacy to distinguish key uncertainties. Its utility thus remains complimentary to quantitative methods, as originally proposed. Ultimately, our ability to predict the consequences of a perturbation rests on empirical factors that remain poorly addressed by our current understanding: how well can we measure interaction strengths, what are the key network elements that confer predictive success, and how compartmentalized are ecological networks? Each of these considerations will also control our ability to assess the stability of ecological communities. More generally, our results suggest that efforts to predict community-wide consequences of even very targeted perturbations must seek to address parameter uncertainty, and hence predictive uncertainty, rather than assuming that network predictions are robust to either the structure or interaction strengths that characterize a community of interest. Thus, until further work is able to sharpen our predictive methods, cautious and adaptive management approaches may be more important than the holistic modeling of nature's complexity itself.

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APPENDIX A

Calculating the weighted-predictions matrix of loop analysis (*Ecological Archives* E092-072-A1).

APPENDIX B

The topological properties of the empirical food webs, and comparisons of qualitative vs. quantitative predictions, aggregated vs. non-aggregated food webs, and alternative parameterizations and richness-connectance levels (*Ecological Archives* E092-072-A2).

APPENDIX C

Mathematica commands for calculating the weighted predictions matrix (*Ecological Archives* E092-072-A3).

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 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).

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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					% Correct predictions ⁷	Ref.
	S^1	L^2	C_I^3	C_d^4	S^1	L^2	R^5	C_I^3	C_d^4		
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.

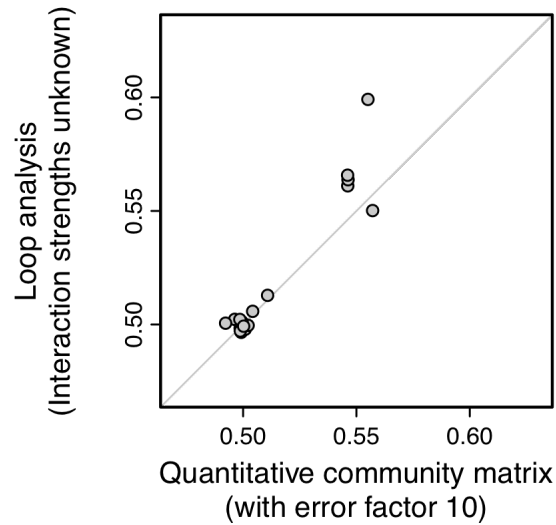


Figure B.1 Correspondence in the empirical food webs between the proportion of correct predictions made by loop analysis (when interaction strengths are unknown), and those made by using the quantified community matrix when interaction strengths are estimated to within an order of magnitude as in Figure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

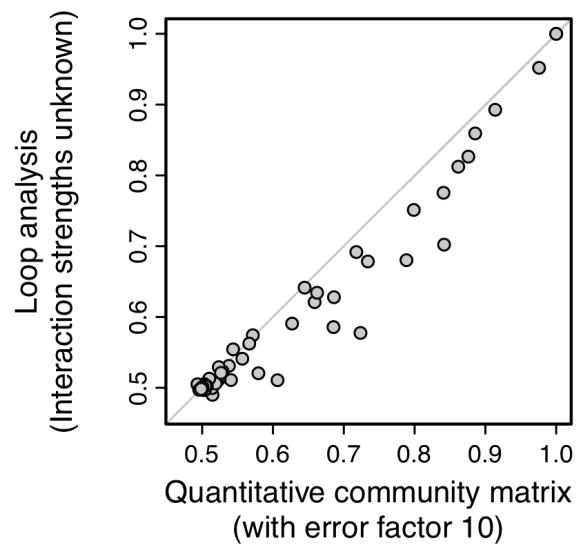


Figure B.2. Correspondence in the niche model food webs between the proportion of correct predictions made by loop analysis (when interaction strengths are unknown), and those made by using the quantified community matrix when interaction strengths are estimated to within an order of magnitude ($r^2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

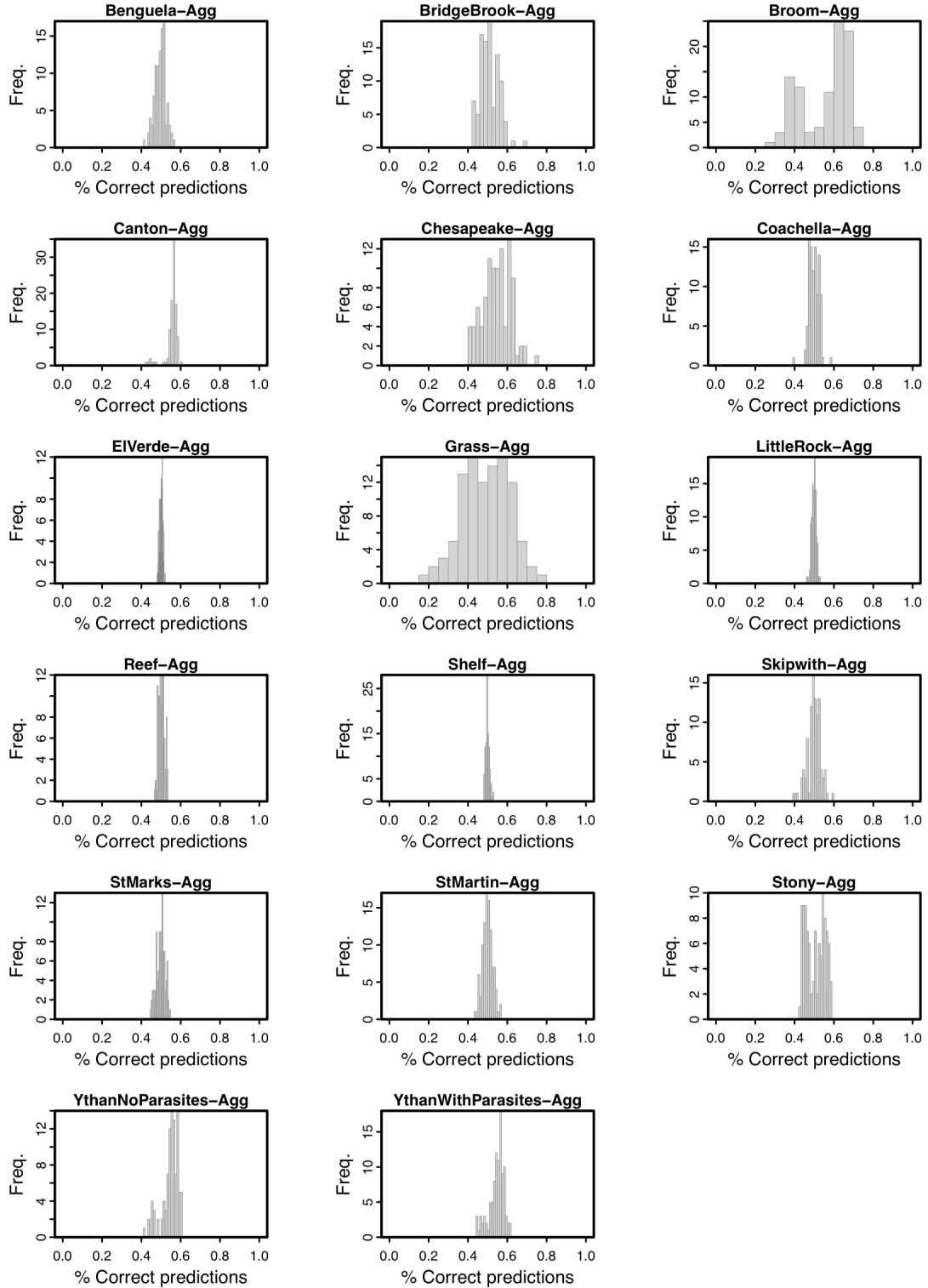


Figure B.3. Frequency histograms of the proportion of correct predictions made across 100 replicate interaction strength realizations of each network's quantified community matrix when interaction strengths estimated to within an order of magnitude error ($F = 10$). The means of these distributions correspond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

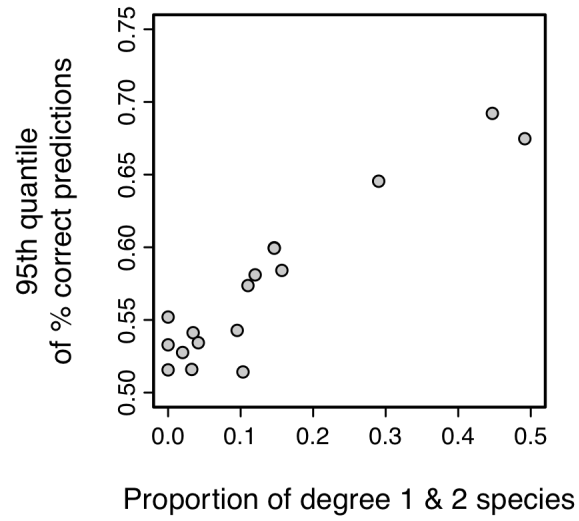


Figure B.4. Across all 17 empirical food webs, the upper 95th quantile of the proportion of correct predictions made using the quantified community matrix (with interaction strengths estimated to within an order of magnitude, $F = 10$) is well-explained by the proportion of species in the food web that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

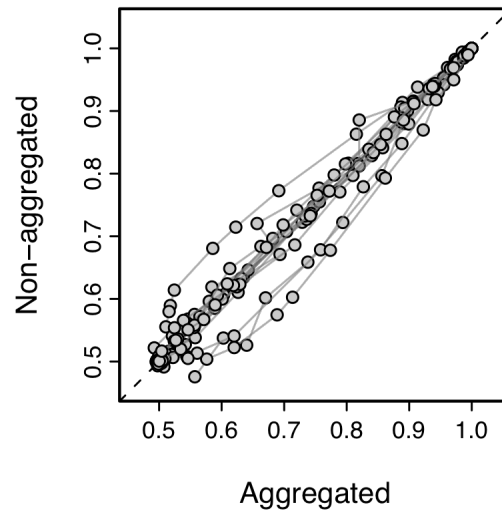


Figure B.5. The relationship between the mean predictive success of aggregated and non-aggregated empirical food webs. Connected points correspond to each of the 17 empirical food webs across successive levels of interaction strength estimation error. The main text presented analyses performed on webs 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.

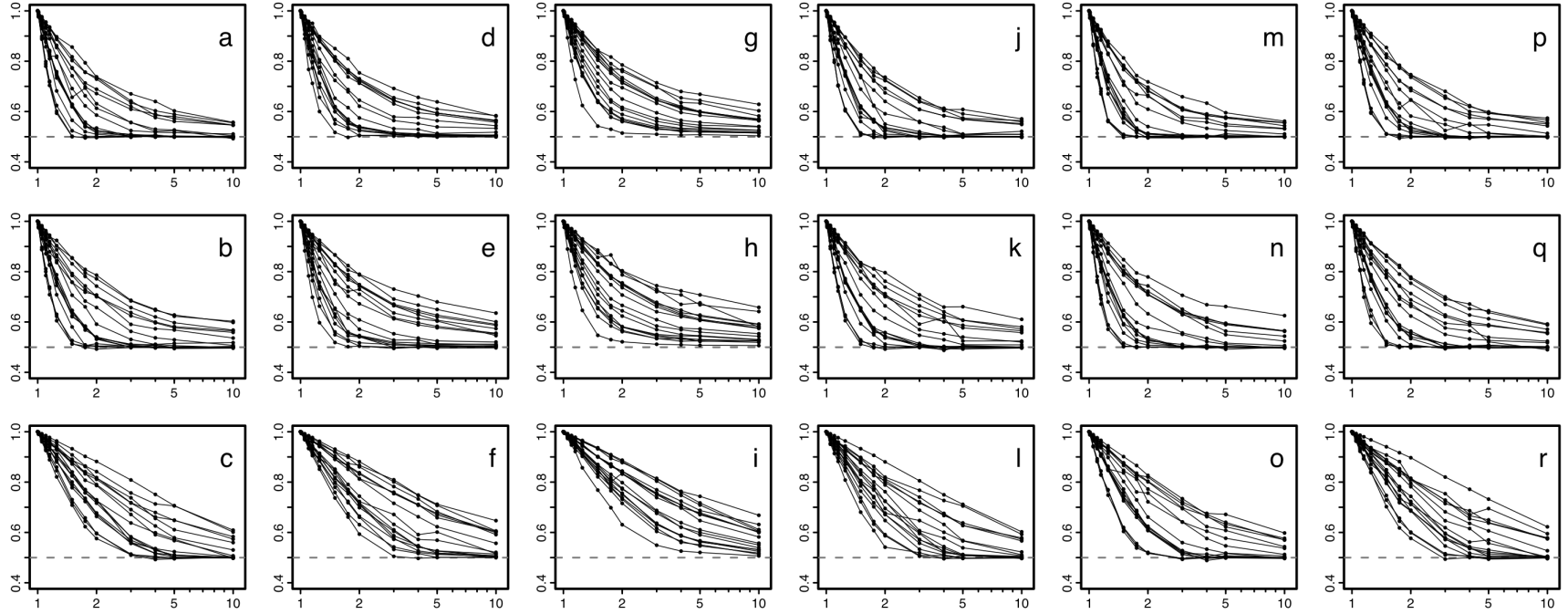


Figure B.6. Sensitivity of results to chosen interaction strength parameters. The mean proportion of correctly made qualitative predictions of species responses declines as a function of the error by which hypothetical interspecific interaction strengths are estimated in 17 well-characterized empirical 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.

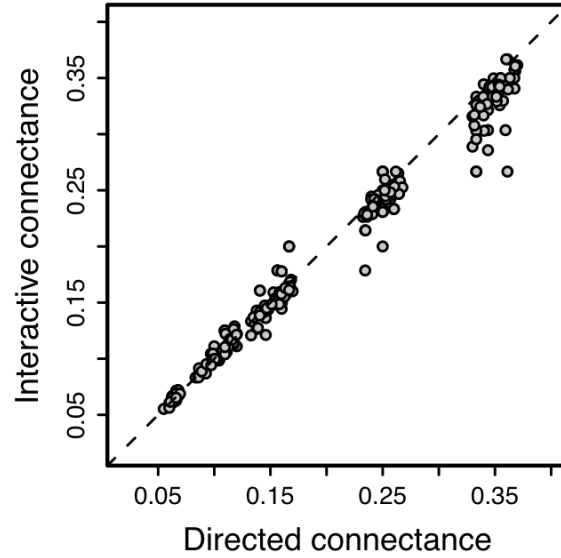


Figure B.7. To avoid the potential confusion introduced by assigning self-limitation effects to all species we illustrate the correspondence between the directed connectance (C_d) by which the complexity of the niche model food webs was specified and the interactive connectance (C_I) of their corresponding 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.

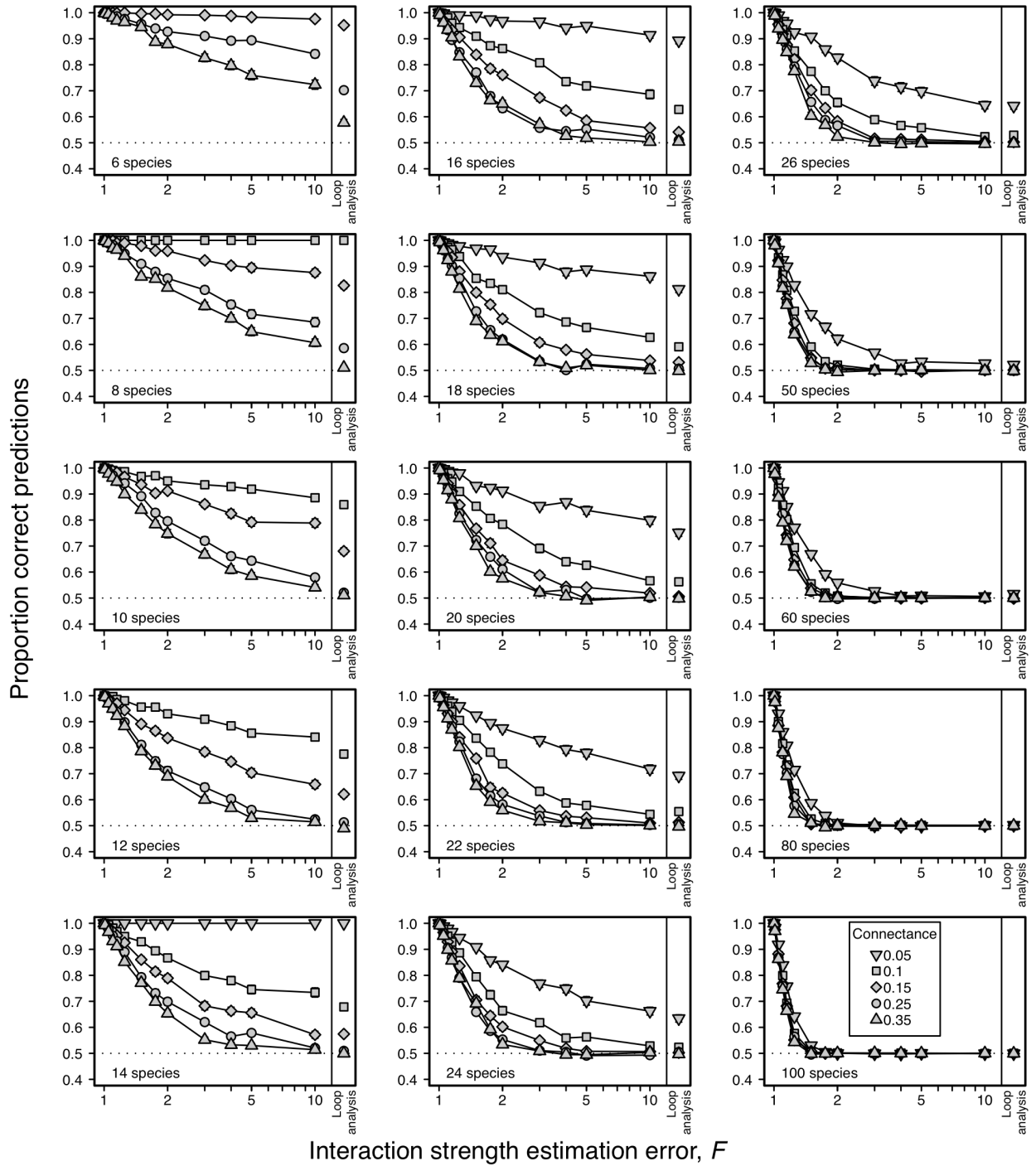


Figure B.8. The mean proportion of correctly made qualitative predictions of species responses as a function of the error by which interspecific interaction strengths are estimated in model communities of increasing size and complexity. An error factor of 1 corresponds to no estimation error, while an 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.

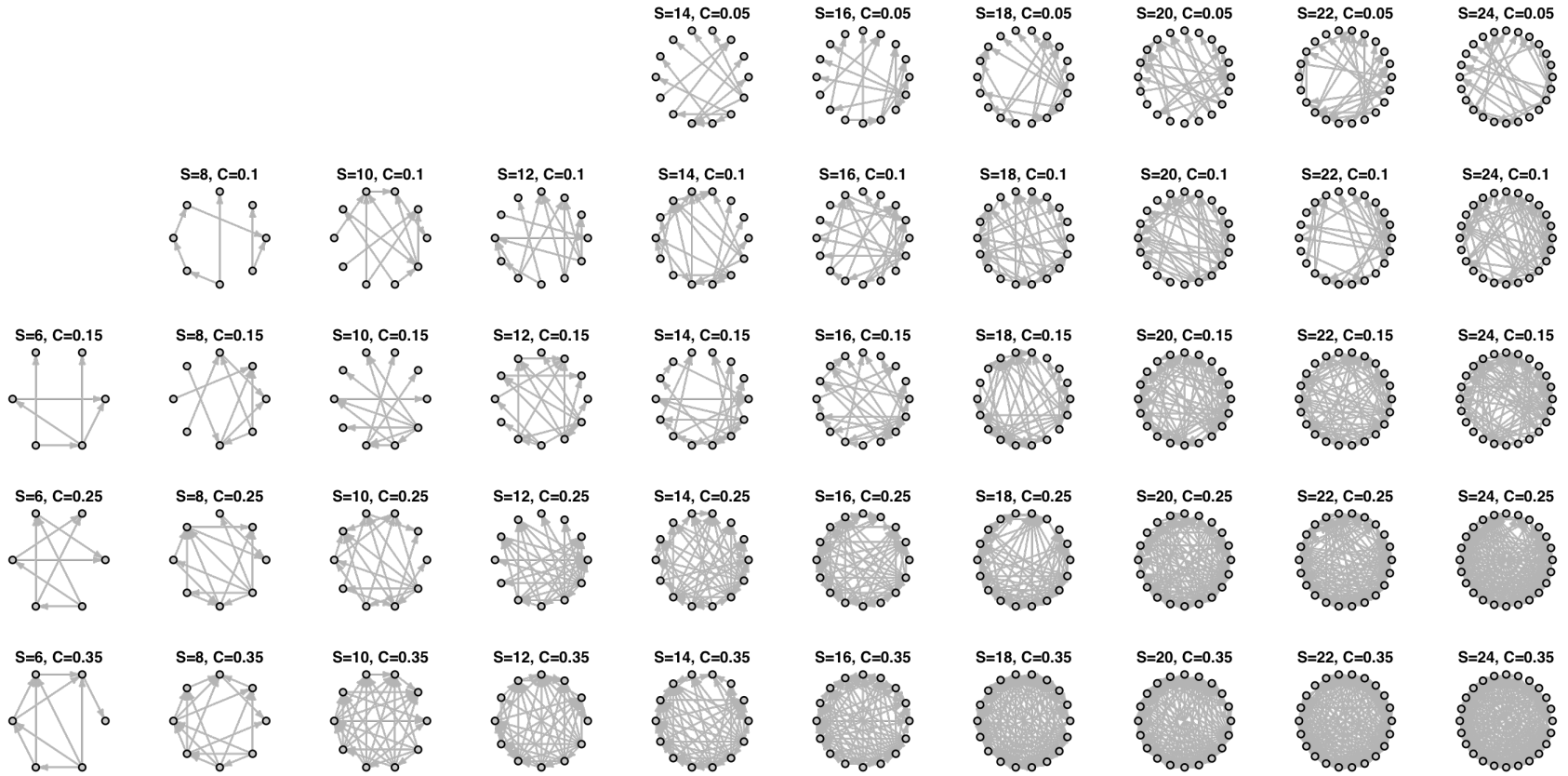


Figure B.9. Examples of the stochastic realizations of the niche model algorithm for each of the investigated species richness (S) and connectance level (C) combinations.

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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
```