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Complexity Increases Predictability in Allometrically Constrained Food Webs

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ABSTRACT: All ecosystems are subjected to chronic disturbances, such as harvest, pollution, and climate change. The capacity to forecast how species respond to such press perturbations is limited by our imprecise knowledge of pairwise species interaction strengths and the many direct and indirect pathways along which perturbations can propagate between species. Network complexity (size and connectance) has thereby been seen to limit the predictability of ecological systems. Here we demonstrate a counteracting mechanism in which the influence of indirect effects declines with increasing network complexity when species interactions are governed by universal allometric constraints. With these constraints, network size and connectance interact to produce a skewed distribution of interaction strengths whose skew becomes more pronounced with increasing complexity. Together, the increased prevalence of weak interactions and the increased relative strength and rarity of strong interactions in complex networks limit disturbance propagation and preserve the qualitative predictability of net effects even when pairwise interaction strengths exhibit substantial variation or uncertainty.

Keywords: net-effects matrix, community matrix, press perturbations, species interaction strengths, complexity, networks.

Introduction

It is widely appreciated that the dynamics of complex ecosystems are sensitive to species interaction strengths and that the vast majority of interactions are weak (Wootton and Emmerson 2005). The influence of this skewed distribution of interaction strengths has seen much scrutiny in the context of uncovering the effects of complexity on network stability and species persistence in the face of acute perturbations (May 1972; McCann 2000; Brose et al. 2006*b*; Tang et al. 2014). In contrast, how interaction strengths and network complexity influence the determinacy, and thereby predictability, of species responses to chronic perturbations remains underexamined (Yodzis 2000; Ives and Carpenter 2007; Novak et al. 2011; Barabás et al. 2014) yet underlies many applications, ranging from fisheries management to climate change research (Sutherland et al. 2009; Travis et al. 2014).

Whether it is in fact possible to predict the dynamics of nature's complex ecological systems or whether hypersensitivity and context dependency will rule the day remains unclear (Lawton 1999; Simberloff 2004; Doak et al. 2008; Beckage et al. 2011; Godfray and May 2014; Petchey et al. 2015; Schindler and Hilborn 2015). Although some models have successfully captured the dynamics of highly resolved communities (Berlow et al. 2009; Boit et al. 2012), others have shown predictive capacity to be severely limited by a combination of network complexity (size and connectivity) and the accuracy to which species interaction strengths are known. These show that even moderate amounts of intrinsic variation or estimation error can routinely reverse whether a species will increase or decrease in abundance after the onset of a perturbation elsewhere in its network (Yodzis 1988, 2000; Abrams et al. 1996; Montoya et al. 2009; Novak et al. 2011). Such poor qualitative predictability (or "directional indeterminacy") stems from the many direct and indirect pathways along which perturbations propagate to determine each species' net response. Even low-complexity networks can be highly indeterminate without accurate knowledge of interaction strengths (Dambacher et al. 2002). Given that (1) the number of possible indirect pathways increases geometrically with network size (Borrett and Patten 2003), (2) indirect effects propagate rapidly (Menge 1997), (3) empirical interaction strengths are associated with both substantial natural variation and estimation uncertainty (Berlow et al. 2004; Wootton and Emmerson 2005), and (4) real ecological systems are much more complex than current food web reconstructions reflect, predictive success should be extremely difficult to achieve (Yodzis 2000; Wootton 2002).

Here we challenge this notion by demonstrating the existence of a positive relationship between network complex-

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ity and the skew of the interaction strength distribution, whose beneficial influence on the determinacy and consequent predictability of food webs increases with network size. Specifically, we show how the indeterminacy caused by indirect effects declines with increasing network complexity when universal allometric constraints associated with species' body sizes determine pairwise interaction strengths. The higher prevalence of weak interactions and the increased strength of strong interactions that results in complex networks when interaction strengths are allometrically constrained preserve predictability even when pairwise interaction strengths exhibit substantial variation.

Methods

We define a network's determinacy, and thereby its predictability, as the directional consistency by which species respond to press perturbations of their community (Yodzis 1988). Net effects between species having high predictability exhibit low directional sensitivity to variation in their constituent interactions. Predictability thereby reflects the ability to anticipate a species' qualitative net response to a press perturbation despite intrinsic variation or estimation uncertainty in the pairwise direct interaction strengths of a community.

Our approach to evaluating the predictability of networks of varying complexity combined the numerical methods of allometric trophic network models (Williams and Martinez 2004) with the analytical efficiency and insights afforded by community-matrix methods (Yodzis 1988; Higashi and Nakajima 1995). In the following we describe (1) how the community matrix may be used to infer species' net effects on each other, (2) how we parameterized community matrices reflecting networks of varying complexity, using allometric trophic network models, and (3) how we quantified the predictability of these networks in the face of interaction strength uncertainty. We then describe how we used (4) randomization experiments and (5) a path-partitioning analysis to assess the mechanisms by which predictability is preserved in complex networks when interaction strengths are allometrically constrained.

Community Matrix

Use of the community matrix (**A**) is well established in the context of the diversity-stability debate (May 1972; Tang et al. 2014). The community matrix is defined by the pairwise partial derivatives of the *i*th species' growth rate with respect to the biomass of species *j* (or "Jacobian matrix"), typically evaluated at equilibrium biomass densities, B^*:

$$\mathbf{A}_{ij} = \left.\frac{\partial(\mathrm{d}B_i/\mathrm{d}t)}{\partial B_j}\right|_{B^*}. \tag{1}$$

Each *ij*th element of **A** reflects the first-order direct effect by which a small increase in species *j* will affect the population growth rate of species *i*, the sign and magnitude of which we here refer to as a "direct interaction strength." Representing only the first nonzero term of a Taylor series approximation to the total direct effect that species *j* has on species *i* (contained within $\mathrm{d}B_i/\mathrm{d}t$), the community matrix ignores all higher-order (nonlinear) terms.

Net effects between two species in a network result from the combined influence of direct and indirect effects. Our use of the community matrix employs the fact that the negative of the inverse of the community matrix ($-\mathbf{A}^{-1}$, henceforth the "net-effects matrix") encapsulates the net response of all species to independent press perturbations of each species as these perturbations propagate through the direct and indirect pathways connecting each species pair (Yodzis 1988). Use of the net-effects matrix is predicated on the assumption that perturbations are sufficiently small or that the pairwise direct effects between species are sufficiently linear near steady state to be well approximated by the community matrix (Bender et al. 1984; Yodzis 1988; Novak et al. 2011). The sign structure of the net-effects matrix describes species *i*'s qualitative response (i.e., increase, decrease, or neutral) to a chronic increase of species *j*'s growth rate.

Allometrically Constrained Interaction Strengths

Previous uses of community-matrix methods have assigned pairwise interaction strengths to community matrices from static distributions (Yodzis 1988; Montoya et al. 2009; Novak et al. 2011) or have assumed that species equilibrium abundances are directly governed by their body sizes (Tang et al. 2014). Instead, we assumed that species' interactions strengths, and thereby also their equilibrial biomass densities, are governed by allometric scaling rules that relate species' body sizes to their metabolic, growth, and maximum ingestion rates (Brown et al. 2004). We did so by using allometric trophic network (ATN) models that extend the bioenergetic consumer-resource model of Yodzis and Innes (1992) to multispecies networks (Williams and Martinez 2004; Williams et al. 2007). ATN models have seen frequent application in the context of understanding network stability and persistence (Brose et al. 2006*b*). They have also seen recent success in explaining the effects of species extinctions (Berlow et al. 2009) and the seasonal dynamics of real ecological communities (Boit et al. 2012).

Our use of ATN models entailed a 3-step process. We first used the niche model to create networks of varying size and connectance (Williams and Martinez 2000) and then assigned body masses to all species on the basis of empirical distributions of consumer-resource mass ratios (Brose et al. 2006*a*). Finally, we used a system of ordinary differential equations to relate network structure and body masses to species dynamics in order to obtain equilibrium biomass densities and the elements of a given network's community matrix.

The niche model requires only the specification of network size (the number of species, S) and trophic connectance ($C = L/S^2$, the proportion of all possible feeding links between species, including cannibalism), randomly assigning each species a value and a feeding range along a 0–1 "niche axis." Although not intended to represent only body size, the niche axis is often interpreted as such because of the dominant effect that body size has on food web structure (Allesina 2011; Stouffer et al. 2011). Increasing connectance increases the width of the feeding ranges and the resulting generality of the consumer species. Those species whose feeding range does not encompass the niche value of another species are considered primary producers. We used only networks with at least 10% of species as primary producers and ensured that all species were connected in one network, creating 5,000 networks with initial richness levels of 10, 20, 30, 40, 50, or 60 species and initial connectance levels of 0.05, 0.15, 0.25, or 0.35. Final richness and connectance levels differed from these initial levels, depending on the number of species that became extinct during simulations. We therefore report results by categorizing networks into bins of varying size and connectance (e.g., connectance ± 0.05).

Species body sizes were assigned on the basis of their trophic level, which was calculated from network structure alone (Levine 1980). Producers were set to a body mass of 1, meaning that our models most closely resemble pelagic systems where primary producers have small body masses and fast turnover rates relative to their consumers. Primary-consumer body masses were assigned by taking a random draw from lognormal empirical distributions of consumer-resource body mass ratios ($\log_{10}(M_{\mathrm{C}}/M_{\mathrm{R}})$) for invertebrates (mean: 0.65, SD: 1.52; Brose et al. 2006*a*). For secondary-consumer body masses, we rounded trophic levels to the nearest integer, subtracted 1, and took the product of that many random draws from a lognormal empirical distribution for ectotherm vertebrate consumer-resource body mass ratios (mean: 2.73, SD: 1.60). Here the standard deviation was divided by the square root of the number of draws to prevent inflation of the sample standard deviation. The resulting distributions of species body masses were reflective of the wide range of variation seen in the real world (fig. A1; apps. A–D and figs. A1, B1, C1, and D1 available online).

The system of ordinary differential equations governing the dynamics of ATN models describe the growth rate of species i's biomass density (B_i) as

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = \overbrace{\sum_{j=1}^{n} x_i y B_i F_{ji}}^{\text{resource gain}} - \overbrace{\sum_{k=1}^{m} x_k \left(\frac{y}{e_i}\right) B_k F_{ik}}^{\text{consumer loss}} - \overbrace{x_i B_i}^{\text{metabolic loss}} \tag{2a}$$

when it is a consumer and as

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = \overbrace{\varepsilon x_i B_i G_i}^{\text{production gain}} - \overbrace{\sum_{k=1}^{m} x_k \left(\frac{y}{e_i}\right) B_k F_{ik}}^{\text{consumer loss}} - \overbrace{(1-\varepsilon) x_i B_i}^{\text{metabolic loss}} \tag{2b}$$

when it is a primary producer (see table 1 for a summary of model parameters). Changes in the biomass density of a consumer species i (eq. [2a]) thus reflect its energetic gains from the consumption of n resources, minus its energetic losses due to consumption by m consumers and its own mass-specific metabolic rate, x_i (i.e., respiration). Changes in the biomass density of primary producers (eq. [2b]) are similarly constrained, except that we assumed growth to follow a logistic growth function,

$$G_i = \frac{(1 - \sum c_{ij} B_j)}{K}, \tag{3}$$

with equal competition coefficients for all j producers ($c_{ij} = 1$) and a constant, system-wide carrying capacity ($K = 10^6$) for all networks (Boit et al. 2012).

The function F_{ji} represents the consumer's multispecies functional response and describes the fraction of i's maximum rate of ingestion that is realized in the consumption of resource j:

$$F_{ji} = \frac{\omega_i B_j^q}{B_0^q + B_i B_0^q + \sum_{l \neq j}^{n} \omega_i B_l^q}. \tag{4}$$

Here F_{ji} depends not only on the biomass density of the focal resource but also on the biomass densities of the consumer's other resources, in a manner that affects a diffusion of a generalist consumer's resource-specific ingestion rates relative to those of a specialist consumer. Consumers were assumed to exhibit uniform resource preferences, $\omega_i = 1/n$, for each of their n resources, which results in consumers encountering and attacking resources in proportion to their biomass density, B_j. For all consumer-resource pairs we assumed the same consumer half-saturation density, $B_0 = 1{,}500$ (Boit et al.

Table 1: Summary of allometric trophic network model parameters

Parameter	Description
B	Species-specific biomass density
x	Species-specific metabolic rate
y	Consumer maximum ingestion rate
e	Assimilation efficiency
ε	Producer carbon-use efficiency
c	Competition between specific producers
K	Carrying capacity
ω	Consumer preference for specific resources
B_0	Half-saturation density
q	Hill exponent
a	Allometric normalization constant
M	Species-specific body mass dependent on trophic level

2012) and set the Hill exponent to $q = 2$ to affect a saturating Type III–like functional response (Brose et al. 2006*b*). The multispecies nature of the functional response also causes an interaction modification (sensu Wootton 1994*a*; Kéfi et al. 2012) in the form of an apparent mutualism between a consumer's resources (Abrams and Matsuda 1996). Apparent mutualisms increase the dynamical connectance of a community above its trophic connectance (app. B) and increase the proportion of positive interactions within the community matrix (Yodzis 2000).

Allometric constraints are incorporated into the ATN framework through the scaling of process rates to species body masses, M_i. Metabolic rates, x_i, follow a negative-quarter-power-law relationship, such that

$$x_i = a_i M_i^{-0.25} \tag{5}$$

(Brown et al. 2004). Following Brose et al. (2006*b*), we set the allometric constant a_i to 1 for all primary producers, 0.314 for all primary (invertebrate) consumers, and 0.88 for all higher (ectotherm vertebrate) consumers. Metabolism-dependent rates of consumption, production, and respiration follow accordingly. The consumer maximum ingestion rate, $y = 10$ (Boit et al. 2012), is expressed per unit metabolic rate, with e representing the assimilation efficiency of herbivorous ($e = 0.45$) or carnivorous ($e = 0.85$) interactions (Brose et al. 2006*b*). Producer production and respiration are expressed as fractions of metabolism, with ε representing the fraction of metabolism allocated to growth (i.e., carbon-use efficiency, $\varepsilon = 0.83$) and $1 - \varepsilon$ reflecting the fraction lost to respiration (López-Urrutia et al. 2006). With the body masses of all primary producers set to 1, the metabolic rate of producers defines the timescale of the system's dynamics.

Our numerical integration of equations (2a) and (2b) for networks of varying complexity used a Runge-Kutta method with adaptive step sizes implemented in Matlab (rel. 2012b; MathWorks). Initial starting biomass densities were set to 1 for all species. If at least 80% of species persisted after 3,000 time steps (biomass densities $> 10^{-30}$; Brose et al. 2006*b*), "extinct" species were removed and numerical integration was repeated until all species persisted. The simulation data underlying all our analyses are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.m27p0 (Iles and Novak 2016). We report our results using final richness and connectance. Equilibrium biomass densities (average biomass densities over the final 200 time steps) were then used to specify the elements of the community matrix and evaluate the network's predictability.

Predictability as Directional Determinacy

Predictability, as defined by directional determinacy, reflects the ability to predict the direction of species' "true" net responses to press perturbations, given intrinsic variation or estimation uncertainty associated with their direct interaction strengths. Thus, having specified a network's community matrix (**A**) on the basis of the ATN framework, we quantified predictability by the proportion of "true" net responses in $-\mathbf{A}^{-1}$ that matched the sign structure of a network's net-effects matrix after varying levels of uncertainty were introduced to the elements of **A** (Novak et al. 2011). To introduce uncertainty we randomly drew new A_{ij} values with equal probability from uniform distributions either above or below their true (no-error) value. That is, the added uncertainty resulted in either an overestimate, Unif $(A_{ij}, A_{ij} \times E)$), or an underestimate, Unif $(A_{ij}/E, A_{ij})$, of each A_{ij} element, with E representing the maximum possible proportional uncertainty, which varied from 1 (no error) to 10 (an order-of-magnitude error). The maximum possible error at each E level was therefore proportional to the magnitude of the true interaction strength. Equivalent results were obtained when we assumed an appropriately scaled and centered lognormal error distribution, and they were predictably affected by altering the assumed proportionality function between uncertainty and interaction strength magnitude (app. C). Uncertainty was introduced either to all interaction strengths or to all except the strongest 5% of interactions to relate to a possible empirical situation whereby the strongest interactions are quantified most accurately. For each network and magnitude of uncertainty, we calculated the average proportion of species net responses that matched the signs of the "true" net responses over 1,000 random iterations.

Randomization Experiments

We next used randomization experiments (Tang et al. 2014) to disentangle the effects of network complexity and interaction strength distributions on predictability. These numerical experiments held the structure of a target network constant but altered its distribution of interaction strengths by drawing new values from source networks of contrasting complexity before reevaluating predictability. We used four target network categories, distinguished by size ($S < 20$ or $S > 50$) and connectance ($C < 0.1$ or $C > 0.3$). Source distributions of direct interaction strengths were obtained by pooling community-matrix elements from networks of 24 possible size-connectance combinations (S = 5–10, 15–20, 25–30, 35–40, 45–50, or 55–60 and $C < 0.1$ or C = 0.1–0.2, 0.2–0.3, or 0.3–0.4). Randomization preserved each target network's topology, sign structure, interaction types (i.e., consumer effects, resource effects, competition between primary producers, apparent mutualisms between resources, and intraspecific effects), and the paired nature of reciprocal consumer-resource interaction strengths, thereby altering only the overall strong-to-weak distribution of interaction strength magnitudes within the community matrices of these target networks as resulting from the ATN simulations. We reassessed the predictability of the target networks assuming an order-of-magnitude level of maximum uncertainty for all interactions ($E = 10$).

Path Partitioning

Finally, we used a path-partitioning approach to investigate the mechanism by which complexity and the distribution of interaction strengths affect predictability. This analysis allowed us to discern the additive influence of indirect pathways of successively longer lengths on the sign of the final net effect between species by decomposing the net-effects matrix ($-\mathbf{A}^{-1}$) with a matrix series expansion:

$$-\mathbf{A}^{-1} = \sum_{l=0}^{\infty} \mathbf{D}^{l}\mathbf{R} \tag{6}$$

(Higashi and Nakajima 1995). Here l is the path length, matrix $\mathbf{D}$ is composed of scaled elements of $\mathbf{A}$ ($D_{ij} = -A_{ij}/A_{ii}$ and $D_{ii} = 0$), and $\mathbf{R}$ is a diagonal matrix with $R_{ii} = -\ 1/A_{jj}$. Our analysis quantified the relative influence of indirect effects of increasingly longer path lengths by the proportion of matrix elements in $-\mathbf{A}^{-1}$ whose sign matched the sign of the corresponding elements in the summed matrix series over successively increasing maximum path lengths (i.e., from $l = 1$, which includes the contribution of only direct effects, to $l = 5$, which includes direct and indirect effects up to a path length of 5).

Results

In contrast to equivalent analyses of networks populated by static, arbitrarily generated interaction strengths (Yodzis 1988; Novak et al. 2011), we find that network predictability increases with higher network connectance (fig. 1*A*–1*C*; compare across lines within each subplot). Thus, while a network's mean predictability declines with increasing network size (fig. 1*A*–1*C*; compare across subplots) and interaction strength uncertainty (fig. 1*A*–1*C*; decline of all lines along the *X*-axis), just as seen in previous analyses (Novak et al. 2011), the rate of decline not only is slower in allometrically constrained networks but also converges on a minimum rate of predictive success that remains better than the 50% (the equivalent of a coin flip) seen in previous analyses (Yodzis 1988; Dambacher et al. 2002; Novak et al. 2011). The positive effect of connectance on predictability is greater in large networks than it is in small networks, particularly when as few as 5% of the strongest interactions are accurately estimated, all others having an order-of-magnitude level of uncertainty (fig. 1*D*–1*F*; compare the spread between lines across subplots). Complexity thereby increases predictability. The influence of complexity on predictability observed in our analyses remains qualitatively unchanged by altering the proportionality function relating interaction strength magnitudes to their uncertainty (app. C). Finally, predictability is related to the overall magnitude of species responses (det(**A**)) but is not explained by variation in asymptotic stability ($\lambda_{\max}$) or matrix condition number ($|\lambda_{\max}/\lambda_{\min}|$; app. D).

The key to why the net effects of more complex networks show improved predictability when pairwise interaction strengths are allometrically constrained lies in how the distribution of interaction strengths changes with network size and connectance. As seen in previous models and in empirical studies (Emmerson and Yearsley 2004; Bascompte et al. 2005; Wootton and Emmerson 2005; Banašek-Richter et al. 2009; O'Gorman et al. 2012), the distribution of interaction strengths in our analyses is highly skewed toward weak interactions (fig. 2). Across the empirically documented range of variation in complexity we explored in our models, this skew becomes more extreme as complexity increases, with the median interaction strength becoming several orders of magnitude weaker (fig. 2) relative to the maximum interaction strengths (fig. 2; change in the span of the bars below each plot). All types of interactions exhibit this tendency with increasing network size as the total available energy-biomass of the system becomes nonuniformly distributed among more species, including the strengths of consumer effects on their resources, resource effects on their consumers, competition between primary producers, apparent mutualisms between resources, and intraspecific effects (fig. 2, *left*). Thus, as network size increases, the strongest interactions become relatively stronger while weak interactions become relatively weaker and more prevalent.

The influence of connectance occurs in two ways. Similar to network size, its first effect is to nonuniformly weaken consumer-resource interaction strengths as the energetic demands and the consequent top-down effects of increasingly generalist consumers are spread more widely across their resources (fig. 2, *right*). This effect is limited to consumer-resource interactions and intraspecific effects, since higher connectance results in stronger producer competition and apparent mutualisms by reducing average biomass densities and increasing the fraction of resource species sharing the same consumers. Increased connectance thereby also reduces the degree of separation between species, by both addition of direct feeding links and proliferation of direct effects between producers and between resource species sharing consumers.

Our randomization experiments show that network predictability increases when a target network's interaction strength values are redrawn from more complex source networks (fig. 3). This positive influence of source network

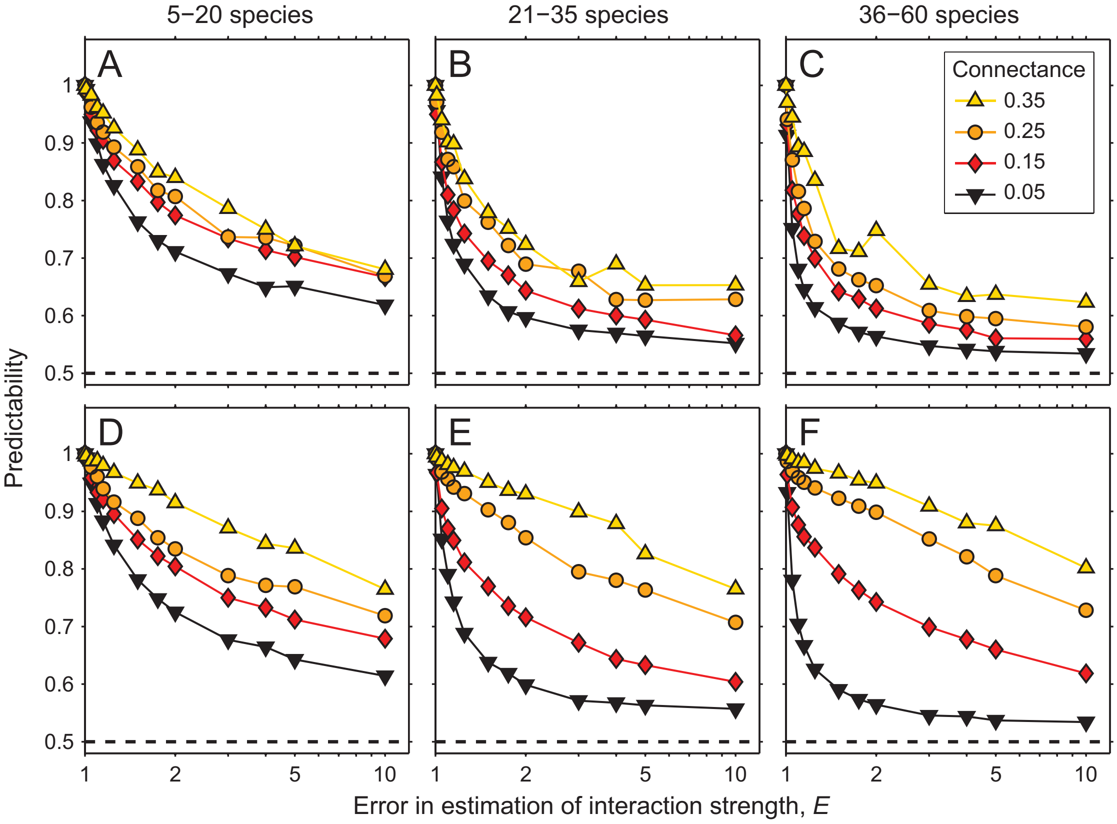

Figure 1: Effects of network complexity on predictability. Network predictability, as assessed by directional determinacy (the mean proportion of net effects with the correct sign), declines with increasing network size and the uncertainty with which species interaction strengths are estimated but increases with network connectance when interaction strengths are allometrically constrained. The positive effect of connectance is magnified in larger networks. *A–C*, All interactions are known with proportionally equivalent magnitudes of uncertainty. *D–F*, Only the strongest 5% of interactions are accurate. For networks of 5–20 species (*A*, *D*), 21–35 species (*B*, *E*), or 36–60 species (*C*, *F*) and connectance levels from 0.05 to 0.35 (±0.05).

complexity on predictability occurs for all target network size-connectance combinations (fig. 3, all panels) but is most evident in highly connected target networks (fig. 3*A*, 3*B*). We hypothesize that this occurs as a consequence of the relative influence of direct and indirect effects. The strength of indirect effects—corresponding to the product of the direct effects along the length of an indirect pathway—diminishes when the source interaction strength distribution is highly skewed. For an indirect effect to be strong, each interaction along the pathway of the indirect effect also must be strong. With a skewed distribution of interaction strengths, the likelihood of this occurring diminishes with the length of the indirect pathway and diminishes faster as the distribution of interaction strengths becomes more skewed. In complex networks, a high prevalence of weak interactions thereby dampens the strength of more counteracting indirect effects, whose opposing signs and similar magnitudes would otherwise generate indeterminacy in the direction of the net effects. Furthermore, with species in highly connected target networks being more likely to be directly connected, there are more direct effects to outweigh the indirect effects. The rarity and increased strength of the strongest interactions mean that relatively fewer links are increasingly responsible for driving most of the perturbation response. As a result, accurately estimating even a small percentage of the strongest interactions has a large influence on predictability in more complex networks (fig. 1*D*–1*F*). Complexity thereby decreases the sensitivity of qualitative predictions to estimation uncertainty by (1) decreasing the degree of separation between species and (2) decreasing the relative influence of most indirect effects while increasing the relative influence of the strongest interactions. Thus, complexity decreases the sensitivity of ecosystems to variation in interaction strengths and increases the consistency with which species affect each other's populations.

The path-partitioning analysis that decomposed the relative influence that pathways of increasing length have on the sign of the net effect between each pair of species supports this hypothesized mechanism. This analysis shows

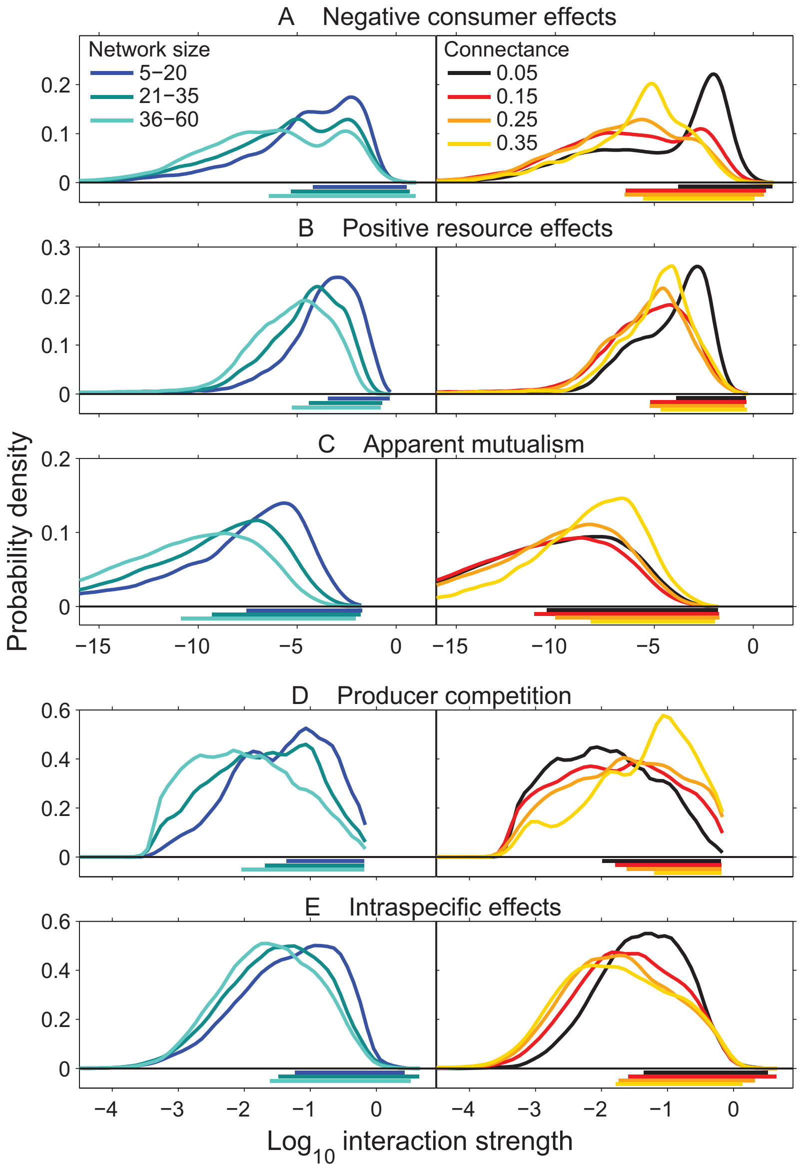

Figure 2: Effects of network complexity on the distribution of interaction strengths. Kernel densities evidence how the distributions of allometrically constrained interaction strengths (depicted by their absolute values) respond to network size (*left*) and connectance (*right*). Interaction strengths are shown separately for negative consumer effects on their resources (*A*), positive resource effects on their consumers (*B*), apparent mutualisms between species that share common consumers (*C*), competition among producers (*D*), and intraspecific self-effects (*E*). Horizontal bars indicate the range from the median to the maximum of each distribution. Note the difference in the *X*-axis scale between *A*–*C* and *D*, *E*.

that, for all network sizes, a greater proportion of the net effects between species match the sign of their direct effects as connectance increases (fig. 4; compare lines within subplots at a path length of 1). That is, while more than 80% of net effects are qualitatively determined by pathways of length 5 or less, the benefit of considering the influence of pathways longer than a single link diminishes with network connectance and increases only slightly with network size. Thus, in more complex networks, species are more likely to be connected directly and the effects of these direct interactions are more likely to dominate the sign of the net effect that species have on each other.

Discussion

Our analyses extend previous insights into the effects of complexity and the skewed distribution of interaction strengths in determining the response of complex ecological systems

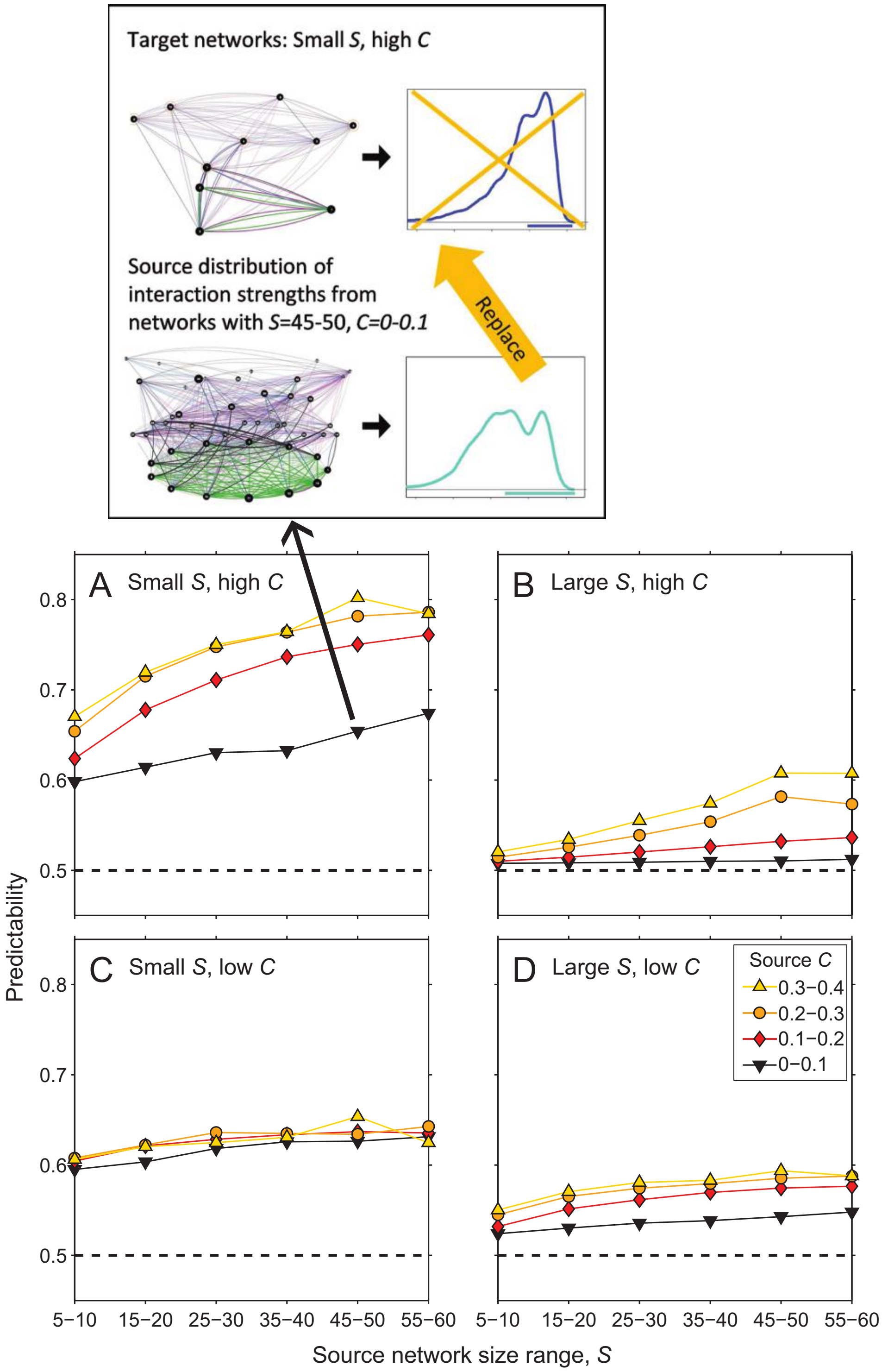

Figure 3: Influence of interaction strength distributions on predictability. The randomized reassignment of interaction strengths between networks of different size and connectance demonstrates that interaction strength distributions drawn from large, high-connectance source networks confer greater predictability to the net effects of target networks of all sizes and connectance levels. Source network size and connectance are respectively indicated by the *X*-axis and differently colored lines. Target networks are categorized by panel into either small ($S < 20$) or large ($S > 50$) size and low ($C < 0.1$) or high ($C > 0.3$) connectance. Predictability is assessed at an order-of-magnitude error ($E = 10$).

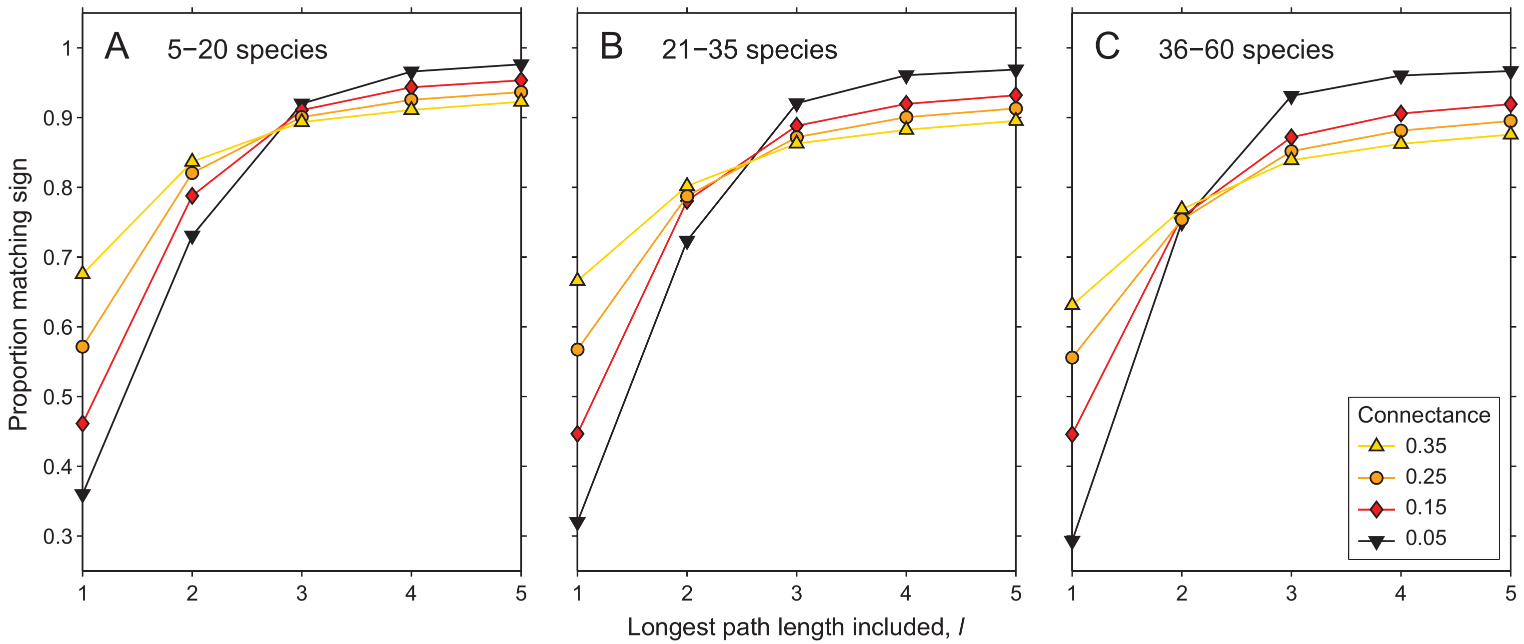

Figure 4: Influence of cumulative pathway lengths on the net effect. Path partitioning reveals how the cumulative influence of increasingly longer indirect effect pathways diminishes relative to that of direct effects for networks of increasing complexity when interaction strengths are allometrically constrained. Along the *X*-axis, the longest pathway considered includes only direct effects between species when $l = 1$, includes direct and 2-step indirect effects when $l = 2$, and so on. The proportion matching the sign of the final net effect is shown for networks of 5–20 (*A*), 21–35 (*B*), and 36–60 (*C*) species for each of four connectance categories (±0.05).

to pulse perturbations (Berlow 1999; McCann 2000; Neutel 2002) to the context of chronic, press perturbations. Although pairs of strongly interacting species are what drive a system's dynamic response to press perturbations, it is the array of weak interactions that determine how far and how strongly perturbations will propagate. By increasing the relative strength of the strong interactions as well as the prevalence of weak interactions that attenuate the propagation of indirect effects, network complexity and allometric constraints make species net responses more consistently tied to the direct effects of the strongest interactions. Our results bear several implications for (1) how complex ecological systems are represented in attempts to understand and predict species responses to chronic perturbations, (2) explaining why many complex ecosystems in nature do exhibit consistent responses to perturbations of their constituent species, and (3) explaining why many communities do not exhibit a greater influence of indirect effects despite their large size.

The foremost implication of our results is that the common practice of simplifying the complexity of ecological systems for the sake of empirical, computational, or analytic tractability—either by aggregating similar species or by ignoring rare species and weak interactions—may unexpectedly be limiting predictive success, altering not only network structure but also the relative representation of weak and strong interactions. To improve our ability to make predictions, we must embrace the complex nature of ecosystems. Although this will remain challenging, our results do suggest optimism, in that parameterizing more complex models to produce qualitatively correct predictions should be easier than previously expected: accurate empirical estimates of only a small fraction of the strongest interactions should improve predictive success, despite high uncertainty in the strengths of the remaining interactions. This is in contrast to previous analyses of networks populated with static interaction strengths, in which removing the error from the strongest 50% of interactions did not substantially improve predictability when all other interactions were estimated poorly (Novak et al. 2011). Methods to identify such "keystone interactions" already exist (Aufderheide et al. 2013; Barabás et al. 2014) and are likely to gain further traction as approaches for inferring interaction strengths on the basis of allometric principles see independent validation (Berlow et al. 2004, 2009; Wootton and Emmerson 2005; Rall et al. 2012).

Our results also help to explain the many consistent ways that real ecosystems respond to chronic perturbations. That is, although ecologists have long emphasized the idiosyncratic, nonlinear, and even chaotic aspects of species dynamics in nature and models, many net effects between species in complex ecosystems exhibit remarkable insensitivity to interaction strength–altering changes in environmental conditions. For example, the pathways of net effects between sea otters and kelp remain qualitatively consistent across large latitudinal gradients in community composition and abiotic conditions that undoubtedly modify and introduce variation in interaction strengths (Estes et al. 2011). Such determinacy in a complex kelp system would not be expected if the structural complexity of ecological networks alone governs ecosystem dynamics.

Empirical distributions of species interaction strengths are known to be skewed (Wootton and Emmerson 2005) and have recently been shown to exhibit heavy tails, similar to the distributions emerging in our simulations (O'Gorman et al. 2012). The extent of this skew and whether it becomes more extreme with network complexity, as seen in our simulations, have not been empirically assessed. Our analyses suggest that a useful proxy may be the observed importance of direct and indirect effects in experiments. An analysis of manipulative experiments in 18 marine rocky intertidal networks found that indirect effects accounted for 22%–68% of the change in community structure (Menge 1995), which broadly encompasses the range of our results (fig. 4). Furthermore, although the number of indirect effects increased with the network size of the species involved in these experiments, their influence on species responses did not (Menge 1995). In light of our results, this suggests that the distribution of interaction strengths became more skewed with network size to counteract the indeterminacy caused by the higher number of indirect effects.

Although our results show a dramatic improvement over previous investigations of predictability in complex ecological networks (Yodzis 2000; Novak et al. 2011), the average predictability of large, low-connectance networks is still quite poor (slightly better than a coin flip). This implies that the relevance of our results may in fact be rather limited, because connectance is thought to decline with increasing network size in empirical food webs (Ings et al. 2009). Our results also suggest, however, that the lower connectance observed in large empirical networks may be an artifact stemming from the difficultly of observing weak interactions, whose prevalence increases in complex networks. If this is correct, then more effort per species would be required to maintain consistent link detectability as network size increases. More empirical work on link detectability across networks of varying size is needed to shed light on this issue.

Our analyses do make several assumptions whose empirical validity requires further scrutiny. First, not all ecological systems will have their dynamics determined by species interactions alone (Mutshinda et al. 2009). Second, additional forms of species interactions not mediated by allometrically constrained trophic relationships are likely also important in determining species dynamics (Kéfi et al. 2012). Third, even within communities whose interactions are allometrically constrained as a general rule, it may be the outlier species, such as sea otters, whose metabolic rate far exceeds that expected for their body mass, that are most critical to dynamics. Finally, the analytical efficiency and insights that are afforded by our use of the community matrix come at the expense of being limited to first-order approximations of species' actual dynamic responses. That is, similar to studies of asymptotic stability in the context of acute perturbations, we too assume that perturbation magnitudes are sufficiently small, or that species responses are sufficiently linear, to have a community's dynamics be well approximated by pairwise linear effects. Our focus on qualitative, directional responses alleviates the severity of this assumption, but how small is sufficiently small remains an open empirical question. Justification is suggested by the success of previous studies using allometric trophic network models to predict the net strengths of species effects after outright species extinctions (Berlow et al. 2009) as well as to describe the seasonally forced dynamics of focal empirical systems (Boit et al. 2012).

Many of the chronic perturbations faced by ecological systems are a consequence of, and of direct relevance to, society's actions. If the interaction strength distributions of real ecosystems do in fact become dominated by weak interactions, with relatively few key strong interactions, as complexity increases, then our capacity to predict and manage the repercussions of these actions may be better than previously thought, once complexity is itself embraced. Conversely, the ongoing biodiversity loss that is simplifying nature's complexity (Butchart et al. 2010) should also be reducing our ability to predict its dynamics. Further effort extending beyond the consequences of biodiversity loss for diversity-stability and diversity-function relationships is needed to continue characterizing our capacity to understand these effects.

Acknowledgments

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Appendix A from A. C. Iles and M. Novak, “Complexity Increases Predictability in Allometrically Constrained Food Webs” (Am. Nat., vol. 188, no. 1, p. 87)

Species Body Mass Distributions

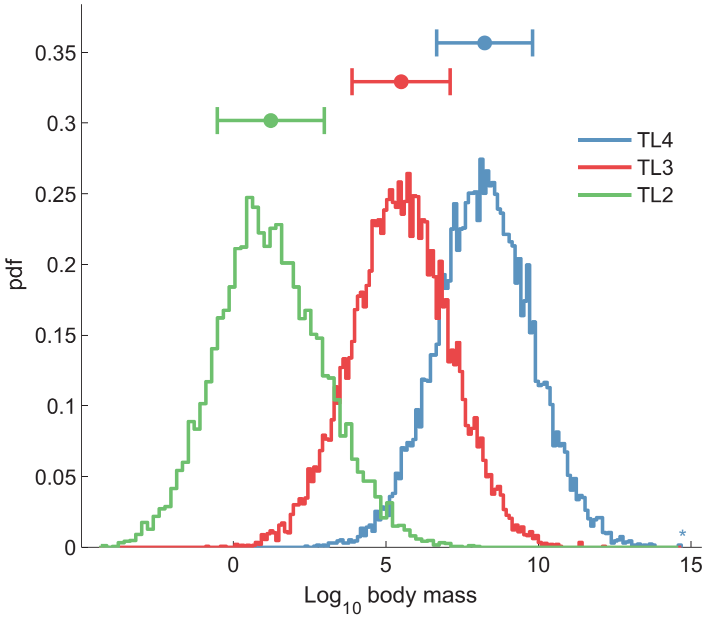

Figure A1: Probability density functions (pdf) of consumer body mass distributions in the allometric trophic network models by trophic level (TL).

Appendix B from A. C. Iles and M. Novak, "Complexity Increases Predictability in Allometrically Constrained Food Webs" (Am. Nat., vol. 188, no. 1, p. 87)

Trophic versus Dynamical Connectance

The measure of connectance we report is trophic connectance, or the proportion of all possible direct feeding links (L) between species (S), $C = L/S^2$. Calculated from the feeding matrix of who-eats-whom, trophic connectance includes only direct feeding interactions of consumers on their resources, including cannibalistic links. Increasing the connectance of a food web results not only in a greater link density but also in a greater proportion of generalist versus specialist consumers. The multispecies functional response describes how the realized fraction of a generalist consumer's maximum ingestion rate is diffused across its resources. The ingestion rate of each resource species depends not only on the biomass density of the focal resource but also on the biomass densities of a generalist consumer's other resources. Thus, the multispecies functional response causes an interaction modification (Wootton 1994*b*; Kéfi et al. 2012), in the form of a weak apparent mutualism in which the presence of an alternate prey modifies the strength of predation for the other prey (Abrams and Matsuda 1996; Yodzis 2000).

Although conceptually apparent mutualisms are an interaction modification, they appear as direct effects in the community matrix because they do not require a change in the biomass density of a third, intermediate species. That is, by the mathematical definition of the community matrix (see "Community Matrix"), its elements represent the direct effect of species j on species i, with all other species abundances held constant. In the case of apparent mutualism, the intermediate species is the consumer that the prey species share in common. Competition between basal producers also appears as a direct effect between producers in the community matrix, even though, conceptually, competition is an indirect effect. In this case, the intermediate "species" is the system's overall carrying capacity, which is shared by all producers. Similarly, intraspecific effects do not depend on an intermediate species. Thus, apparent mutualism, producer competition, and intraspecific effects appear as direct effects in the community matrix.

The dynamical connectance of a network is a measure of connectance that includes all effects as encapsulated by the nonzero elements of the community matrix. These include not only consumer-resource effects but also intraspecific effects, apparent mutualisms, and competition between producers. Dynamical connectance thus reflects both the direct links between species (as reflected in trophic connectance) and any other effects that do not require a numerical response from an intermediate species. We use the term "dynamical" connectance because it is the community matrix that encapsulates the dynamical properties of the system. As opposed to trophic connectance, dynamical connectance reflects the actual pathways along which perturbations propagate. In linear Lotka-Volterra models, dynamical connectance and trophic connectance are equivalent. However, in multispecies allometric trophic network models, as trophic connectance increases consumers feed on wider range of resources, and the resulting dynamical connectance increases even faster (fig. B1).

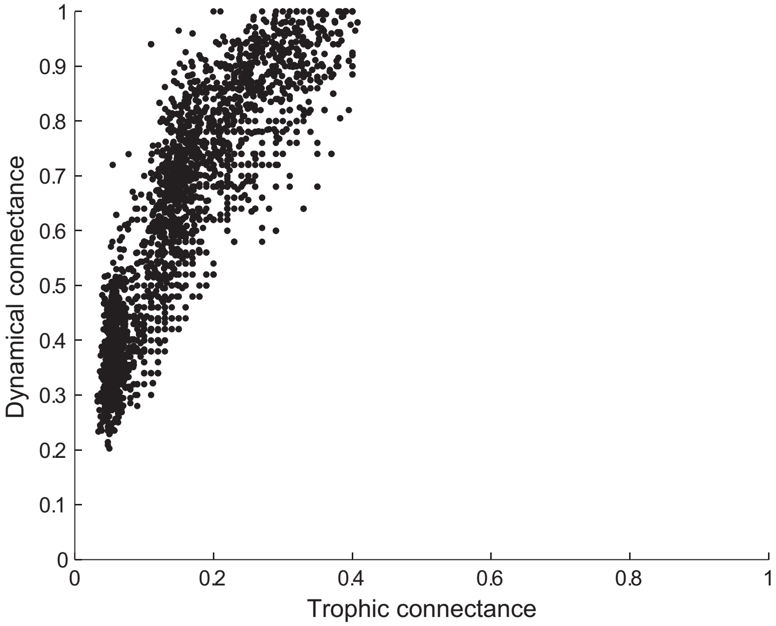

Figure B1: Relationship between each network's trophic connectance and its effective dynamical connectance.

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Appendix C from A. C. Iles and M. Novak, “Complexity Increases Predictability in Allometrically Constrained Food Webs”
(Am. Nat., vol. 188, no. 1, p. 87)

Choosing an Error Distribution for Evaluating Directional Sensitivity

Here we compare our results based on a uniform distribution for the error introduced to species interaction strengths (presented in the main text) to results obtained with a lognormal distribution of error. Both constrain an interaction’s magnitude in such a way as to not alter its sign. The mean of the lognormal error distribution is centered on the interaction strength’s true magnitude. Three functions relating the magnitude of an interaction’s uncertainty to its mean were assessed, as the existing empirical relationship between an estimate’s mean and variance is as yet unknown (but see Berlow et al. 1999): (1) a constant proportional error, F, that was independent of an interaction strength’s magnitude, (2) an increasing proportional error that scaled positively with an interaction’s magnitude, and (3) a decreasing proportional error that scaled negatively with an interaction’s magnitude. For case 1, we specified the standard deviation of the lognormal distribution (σ) to affect a magnitude of proportional uncertainty that corresponded to our results presented in the main text (table C1). For each standard deviation value, the corresponding uniform distribution of the main text captured 99% of the lognormal distribution. For case 2, the smallest nonzero-magnitude $\log_{10}$ interaction strength was given no error ($\sigma = 0$, $F = 1$), while the largest was given an order-of-magnitude error ($\sigma = 0.895$, $F = 10$). The remaining $\log_{10}$ interaction strengths were assigned a standard deviation along this range, in proportion to their magnitude. The same procedure was used in case 3, except that the largest interaction strength was assigned no error ($\sigma = 0$, $F = 1$), while the smallest interaction strength received an order-of-magnitude error ($\sigma = 0.895$, $F = 10$). These analyses show that a lognormal error distribution produces results that are qualitatively similar to the uniform error distribution (fig. C1*A*, C1*B*) yet also highlight how important the scaling relationship between estimation uncertainty and interaction strength magnitude is for evaluating directional insensitivity (fig. C1*B*–C1*D*). If stronger interaction strengths exhibit less variation, as some empirical evidence suggests (Berlow 1999), or are estimated with less uncertainty (fig. C1*D*), then net effects should be highly insensitive to any error in the remaining weak interactions.

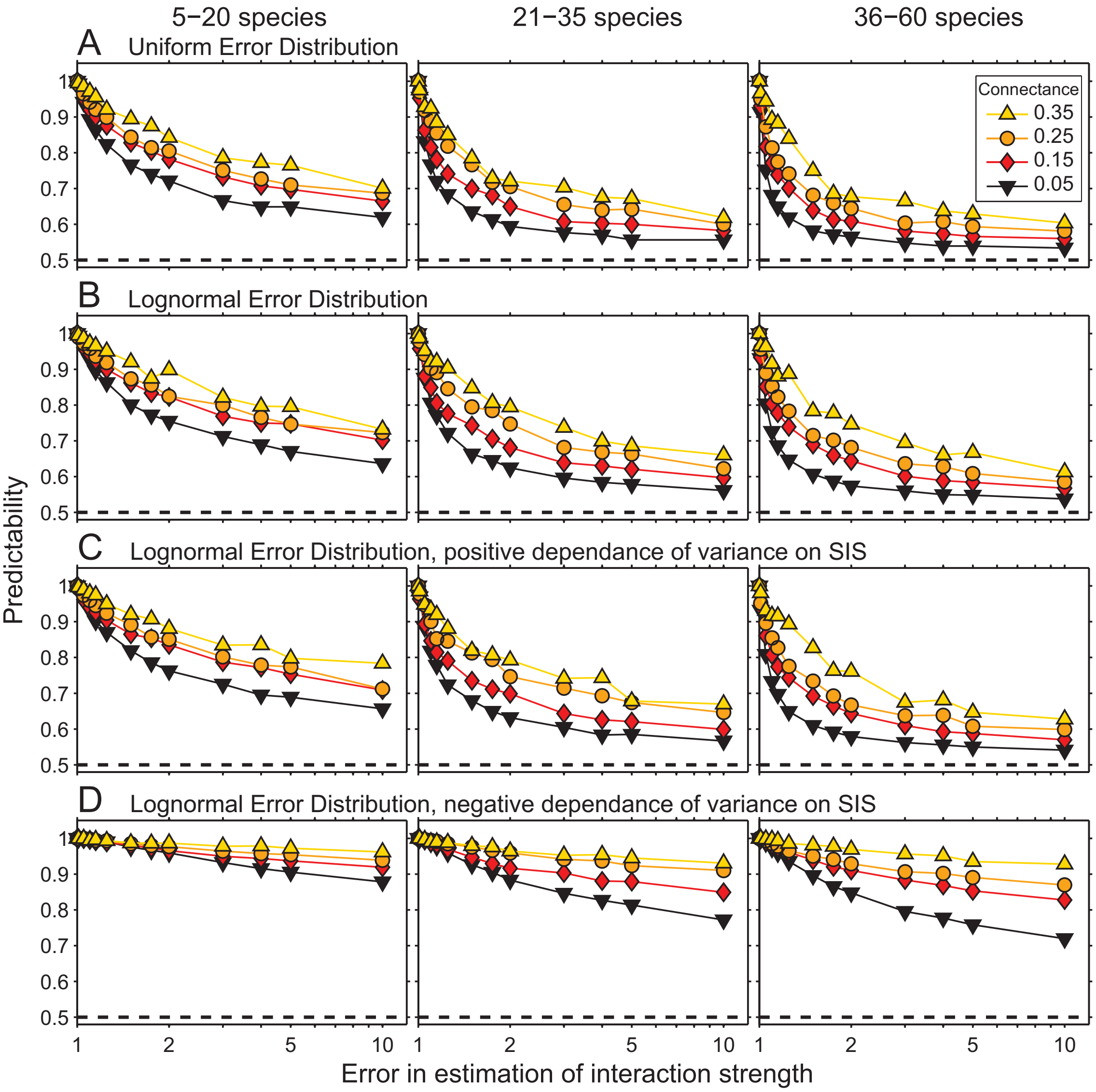

Figure C1: *A*, *B*, Decline in directional insensitivity, or mean proportion of net effects with the correct sign, when all interactions have an equal likelihood of a uniform error distribution (*A*) or a lognormal error distribution with corresponding levels of uncertainty (*B*). *C*, *D*, Lognormal error distributions for which maximum proportional uncertainty is positively (*C*) or negatively (*D*) related to the true magnitude of the $\log_{10}$ interaction strength. SIS = species interaction strength.

Table C1: Standard deviations of the lognormal distribution of interaction strength uncertainties and corresponding *F* values of the uniform error distribution

Proportional error, *F*, of the uniform error distribution	Standard deviation, σ, of the lognormal distribution
1	0
1.01	.0050
1.05	.0190
1.10	.0371
1.15	.0543
1.25	.0867
1.50	.1576
1.75	.2174
2	.2699
3	.4268
4	.5381
5	.6284
10	.8950

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Appendix D from A. C. Iles and M. Novak, "Complexity Increases Predictability in Allometrically Constrained Food Webs" (Am. Nat., vol. 188, no. 1, p. 87)

Predictability Related to Stability, Matrix Condition Number, and Matrix Determinant

Assessing asymptotic stability by the maximum eigenvalue ($\lambda_{\max}$) shows no relationship with predictability, as defined by directional determinacy, or the sensitivity of qualitative predictions to an order-of-magnitude ($F = 10$) variation in interaction strength estimates (fig. D1*A*, D1*D*). The matrix condition number ($|\lambda_{\max}/\lambda_{\min}|$) is often used to quantify the sensitivity of a matrix to inversion. The networks of our analyses were all well conditioned and evidence no relationship between condition number and predictability (fig. D1*B*, D1*E*). The determinant of the community matrix, $\det(\mathbf{A})$, scales the magnitudes of $-\mathbf{A}^{-1}$ and reveals a positive relationship between predictability and the overall magnitude of species responses. Like network predictability, the matrix determinant is sensitive to network size and connectivity (fig. D1*C*, D1*F*).

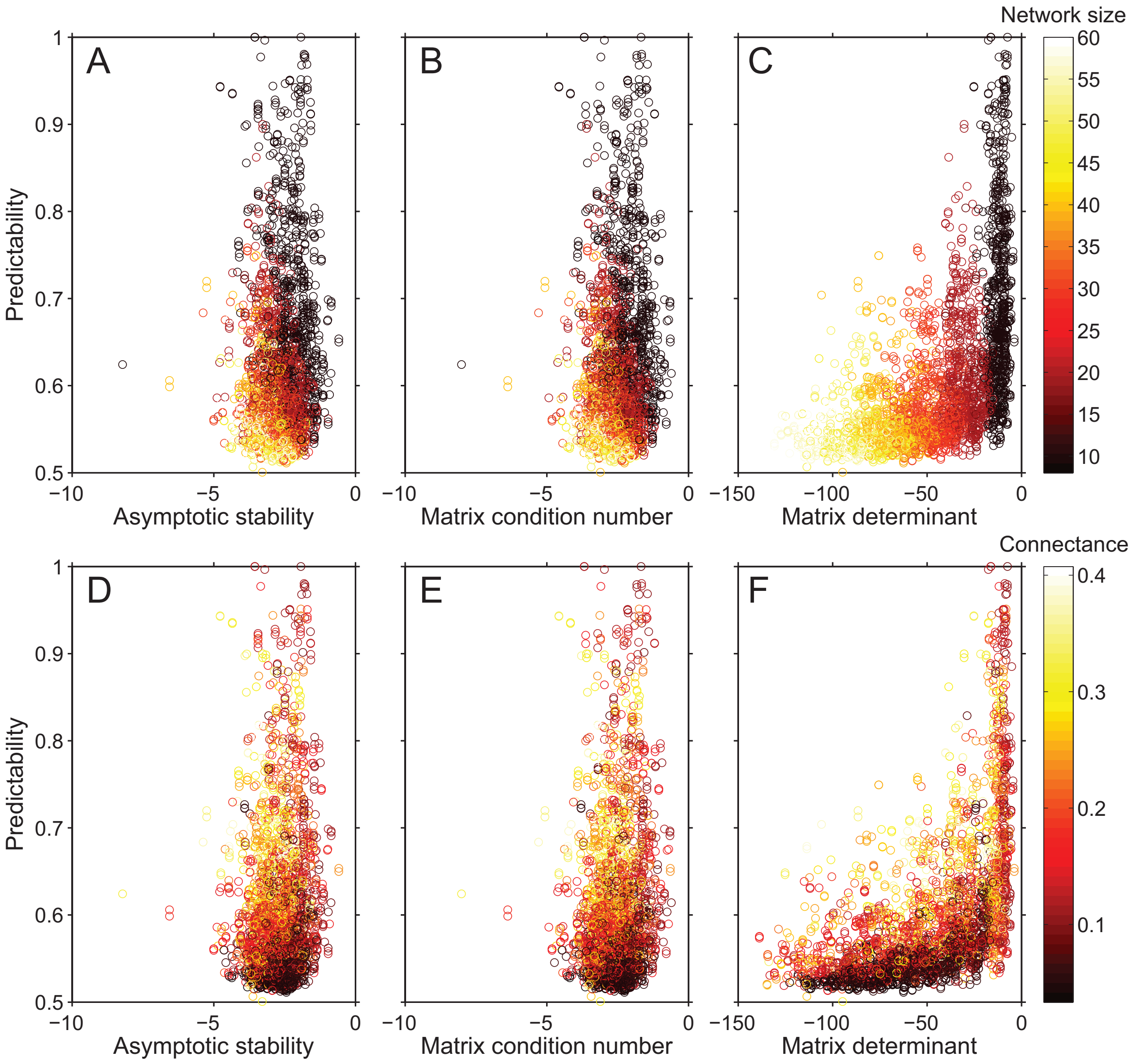

Figure D1: Relationship between network predictability (as measured by directional determinacy) and asymptotic stability ($\log_{10}(|\lambda_{\max}|)$ (*A*, *D*), matrix condition number ($\log_{10}(|\lambda_{\max}/\lambda_{\min}|)$ (*B*, *E*), and the matrix determinant ($\log_{10}(\det(\mathbf{A})$; *C*, *F*) for networks of varying size (*A*–*C*) and connectance (*D*–*F*). Predictability reflects the mean proportion of net effects with the correct sign after up to an order-of-magnitude error is introduced to all interactions ($F = 10$).