

Simple prediction of interaction strengths in complex food webs

Eric L. Berlow^{a,b,c,1,2}, Jennifer A. Dunne^{c,d}, Neo D. Martinez^c, Philip B. Stark^e, Richard J. Williams^{c,f}, and Ulrich Brose^{b,c,2}

^aUniversity of California, Merced, Sierra Nevada Research Institute, Wawona Station, Yosemite National Park, CA 95389; ^bDarmstadt University of Technology, Department of Biology, Schnittpahnstrasse 10, 64287 Darmstadt, Germany; ^cPacific Ecoinformatics and Computational Ecology Lab, 1604 McGee Ave., Berkeley, CA 94703; ^dSanta Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501; ^eUniversity of California Berkeley, Department of Statistics, Berkeley, CA 94720-3860; and ^fMicrosoft Research Ltd, 7 J. J. Thomson Avenue, Cambridge CB30FB United Kingdom

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Darwin's classic image of an "entangled bank" of interdependencies among species has long suggested that it is difficult to predict how the loss of one species affects the abundance of others. We show that for dynamical models of realistically structured ecological networks in which pair-wise consumer-resource interactions allometrically scale to the $3/4$ power—as suggested by metabolic theory—the effect of losing one species on another can be predicted well by simple functions of variables easily observed in nature. By systematically removing individual species from 600 networks ranging from 10–30 species, we analyzed how the strength of 254,032 possible pair-wise species interactions depended on 90 stochastically varied species, link, and network attributes. We found that the interaction strength between a pair of species is predicted well by simple functions of the two species' biomasses and the body mass of the species removed. On average, prediction accuracy increases with network size, suggesting that greater web complexity simplifies predicting interaction strengths. Applied to field data, our model successfully predicts interactions dominated by trophic effects and illuminates the sign and magnitude of important nontrophic interactions.

body size | ecological networks | species extinctions | species interaction strengths | systems theory

I would not give a fig for simplicity on this side of complexity, but I'd give my life for the simplicity on the other side of complexity.

Oliver Wendell Holmes, Jr.

One of the greatest challenges of environmental biology is to predict the effect of human activity on the complex webs of interactions among species. While there has been progress understanding how the extinction of one species may cause further extinctions of other species (1–5), understanding how extinctions may alter the abundances of every species in the web is critical for predicting community-wide responses to external perturbations (6, 7). Many species interactions involve the fundamental need to acquire energy, and well-documented allometric scaling rules describe relationships between body size, metabolism (8, 9), and food consumption (10, 11). Can these scaling rules at the level of individual trophic links help predict the effect of removing one species on others in a realistically structured food web? While nontrophic interactions among species (e.g., habitat modification, interference competition, behavioral modifications) (12, 13) can strongly affect species abundances, the fundamental physiological need for food may provide a null model (14) of species interactions against which the importance of other ecological processes can be assessed.

Some studies suggest that the multiple interaction paths connecting any two species in a realistically complex community will make it impossible to predict the influence of one on the other (15, 16). However, others argue that effects along longer paths should be weak and hence unlikely to interfere with prediction of extinction effects (17). Here, we report numerical experiments that explore how extinctions affect the mean abun-

dances of all other species in models of complex food webs (see *Materials and Methods*). We simulated population dynamics and species removals in 600 food web models with 10–30 species and where all pair-wise consumer-resource trophic interactions are governed by simple allometric scaling rules (1, 18, 19). We explore two general questions: (i) How are per capita pair-wise rules modified by network dynamics? (ii) Is there a simple predictor of the dynamic effect of removing a species on the other species in a network governed by allometric scaling rules? While we focus on the consequences of species extinction, our approach may be extended to less dramatic changes in species abundance (e.g., over-harvesting).

The models are based on five simplifying assumptions: (i) autotrophs or "basal species" compete for fixed inputs of two primary limiting nutrients (20); (ii) the rate of metabolism and maximum per capita consumption (hereafter, "maximum consumption") of all consumers scale with their body mass to the $3/4$ power (10, 21); (iii) consumer-resource body-mass ratios are log-normally distributed with mean 10 and standard deviation 100 (22); (iv) networks are structured according to the "niche model" (23); and (v) generalist consumers feed on different resources in proportion to the resources' relative biomasses (i.e., there is no complex foraging behavior). This Allometric-Trophic-Network (ATN) model simulates population dynamics within food webs following an allometric predator-prey model (18, 21) where:

$$B_i' = r_i G_i(N) B_i - x_i B_i - \sum_{j \in \text{consumers}} x_j y B_j F_{ji} / e_{ji} \quad [1a]$$

$$B_i' = -x_i B_i + \sum_{j \in \text{resources}} x_j y B_j F_{ij} - \sum_{j \in \text{consumers}} x_j y B_j F_{ji} / e_{ji} \quad [1b]$$

describe changes in relative, dimensionless biomass densities of primary producer (Eq. 1a) and consumer species (Eq. 1b). In these equations, B_i is the biomass density of species i , r_i is i 's mass-specific maximum growth rate, G_i describes the nutrient-dependent growth rate for all basal producer species i that compete for the same limiting nutrients (see *SI Appendix*), x_i is i 's mass-specific metabolic rate, y is the maximum consumption rate of the consumers relative to their metabolic rate, e_{ji} is j 's assimilation efficiency when consuming species i . The functional

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¹To whom correspondence should be addressed. E-mail: eberlow@ucmerced.edu.

²E.L.B. and U.B. contributed equally to this work.

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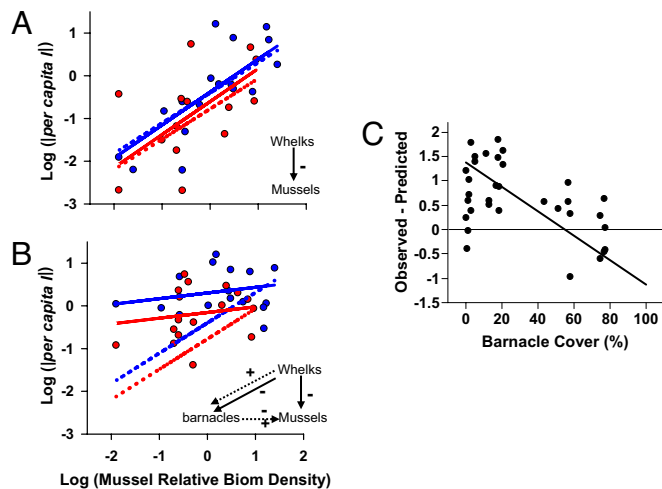


Fig. 3. Empirical test of the metabolic baseline of interaction strengths. \log_{10} per capita I of predatory whelks (R) on mussels (T) depending on $\log_{10}(B_T^+)$ for low (blue) and high (red) levels of R biomass with (A) or without (B) nontrophic influences of barnacles. ATN model predictions (dotted lines) are compared to separate linear regressions through the empirical data (solid lines). In the interaction web diagrams, solid arrows indicate trophic interactions, and dotted arrows indicate nontrophic interactions. Regression models for the empirical data (solid lines) for, A, $R^2 = 0.48$, $\log_{10}(\text{per capita } I) = -0.29 + 0.77 \log_{10}(B_T^+) - 0.47 \log_{10}(B_R)$; B, $R^2 = 0.22$, $\log_{10}(\text{per capita } I) = 0.47 + 0.13 \log_{10}(B_T^+) - 0.96 \log_{10}(B_R)$. (C) The difference between empirically observed \log_{10} per capita I when nontrophic influences of barnacles are present and those predicted by the ATN simulations as a function of mean barnacle cover in paired plots without whelks or mussels. RMA regression: slope = -0.025 , $R^2 = 0.26$.

mussel biomass and over-predicts per capita I at very high mussel biomass (Fig. 3B). The difference between observed I and that predicted by our metabolic-trophic model is explained well by natural variation in barnacle cover (Fig. 3C). The observed negative effects of whelks on mussels were stronger than the model predicts when barnacle cover was low ($<$ approximately 50%), and weaker than predicted when barnacle cover was high ($>$ approximately 75%) (Fig. 3C). At low natural barnacle cover, the nontrophic effect of whelks on mussels is negative because whelks reduce the abundance of barnacles, impeding mussel recruitment. At very high barnacle cover, however, the nontrophic effect of whelks on mussels is positive because whelks stabilize barnacle abundance, which increases mussel recruitment. In sum, the ATN model accurately predicts the effect of whelks on mussels, absent nontrophic facilitation by barnacles. Deviations from the ATN model predictions reveal both the magnitude and sign of the important nontrophic effect. Results for population-level I are almost identical (data not shown). Thus, our simple empirical test of this ATN model successfully predicts a primarily trophic interaction and predictably fails when strong nontrophic effects were present. Similar tests in other systems will help evaluate the strength and generality of this approach.

Discussion

Our ATN simulations elucidate how very general metabolic constraints on trophic relationships play out in theory when consumer-resource interactions are embedded in realistically structured trophic networks. In a complex network, the response of one species to the removal of another does not scale the same way that direct per capita feeding interactions do. However, new simple patterns emerge. That distant effects of long interaction chains are generally weak tends to dampen difficult to predict and otherwise unexpected effects. Our results appear relatively independent of large variation in network structure, consumer-

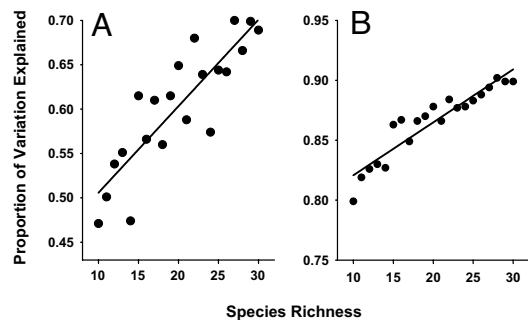


Fig. 4. More complex is more simple. The proportion of variation in (A) $\log_{10} I$ and (B) \log_{10} per capita I explained by the most parsimonious multiple linear regressions described in Figs. 1D and 2C for different levels of species richness that each included a range of connectance values. The absolute magnitude of both I and per capita I explained increases with web size ($R^2 = 0.74$ and 0.88 for A and B, respectively).

resource body mass ratios, consumer functional responses, and other species traits used to model species' population dynamics. These simulations also suggest that in trophic networks, static measures of interaction strengths based on simple species attributes (e.g., body mass and biomass) (6, 11) may be highly correlated with dynamic measures based on removing species. More complex networks had simpler behavior: the proportion of variation in both I and per capita I explained by the set of simple R and T attributes increased approximately linearly with species richness (Fig. 4).

$|I|$ and per capita $|I|$ in our simulations are predicted well by linear models that include the time-averaged biomasses of R and of T as explanatory variables. Predictions using the biomass at a single time would be less accurate if the biomass greatly fluctuates over time. Prior analyses of “keystone” species removal in complex networks (1) focused on one type of positive interaction where the removal of a consumer, R , causes a strong increase in a competitively dominant basal T that, in turn, causes other basal T species to go secondarily extinct. The group of red symbols in Fig. 1A-C represent the small subset of cases where a dominant basal T increases greatly when its only consumer is removed. In cases of secondary extinction of T (1), I has been shown to depend strongly on local network structure with R present. In the more general case explored here, where B_T^- is nonzero, these local network properties do not help much to predict I : attributes of T and R suffice.

Our ATN simulations show how network effects transform a simple allometric rule for pair-wise feeding interactions. The approach could be extended to incorporate additional ecological factors (3, 33) to describe an energetic baseline of species interactions in ecosystems that vary in the importance of environmental stochasticity and spatial and subpopulation scale processes. The predictability of simulated interactions suggests that (i) studies of species interactions that focus on a simple subset of a natural community provide insights that are robust to variation in peripheral network structure; (ii) species' interactions known to be primarily driven by energetics may be predicted well by simple species and network attributes; and (iii) the characteristically variable, “context-dependent,” or “unanticipated” outcomes of species' perturbations in empirical studies (28, 32, 34) may not be due to inherently intractable network influences (15). Instead, this variability may point to other biotic mechanisms (e.g., behavior and nontrophic interactions) (12, 13) or abiotic factors regulating species interactions. Metabolic requirements are critical to all ecological networks, and the predictability of interactions mediated by these requirements makes it possible to assess the relative importance of other ecological processes by examining deviations from ATN predic-

tions (14). More generally, our results suggest that the complexity of natural food webs is tractable and may simplify, rather than complicate, predicting the consequences of species loss.

Materials and Methods

General Approach. We employ four steps to simulate ATN: (i) The niche model (23) generates network structures with random, uniformly distributed species richness (10 to 30) and connectance (0.1–0.2). (ii) Species' body masses are generated, starting with a basal species level of unity. Successively higher levels are generated using average consumer-resource body-mass ratios sampled from a log-normal distribution (mean = 10, SD = 100) (18, 22). (iii) A dynamic consumer-resource model (21) with nonlinear functional responses including random, normally distributed Hill exponents (mean = 1.5, SD = 0.25) and predator interference terms (mean = 0.5, SD = 0.25) is parameterized by random initial biomasses and $3/4$ power-law relationships between the rates of metabolism, maximum consumption, and production and body masses (1, 18) (see *SI Appendix* for model details). (iv) A plant-nutrient model (35) is assigned to the basal trophic level (1, 20). These steps were repeated independently 600 times to generate realistic variation in model parameters defining network structure, predator metabolism, maximum consumption, initial biomass, and functional response, and the nutrient uptake rates of basal species. To analyze the effect of removing each species on the biomass of every other species, each of the 600 dynamic network models was run once with all species present and

subsequently with each species in the network removed in turn. Each species' average biomass per unit area and population density (number of individuals per unit area) from time step 50 to 200 was monitored to calculate I and per capita I (*SI Appendix*). For each removal, we tracked 90 attributes of the global network (e.g., connectance), the local network structure (e.g., the numbers of direct consumers of T and R), the species (e.g., body mass and biomass of T and R), and the pair (e.g., degrees separated) (*SI Appendix*). CART (36) was used to model the sign and magnitude of I and to select explanatory variables for Reduced Major Axis (RMA) regression and multiple linear regression models of $\log|I|$ and $\log|I|$ per capita I . Models were developed using a random sample of half the webs and tested on the other half. Additional simulations of different length suggest that (i) secondary extinctions do not greatly alter the results, and (ii) the general patterns we observe are robust to different simulated times frames (Figs. S3 and S4, Table S1). Empirical data on interaction strengths in a rocky intertidal community were reanalyzed from previously published data (27, 32) [For more methodological details about the ATN model, the time frame of the simulations, the analysis of simulation data, and the application to field data, see *SI Appendix*].

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