

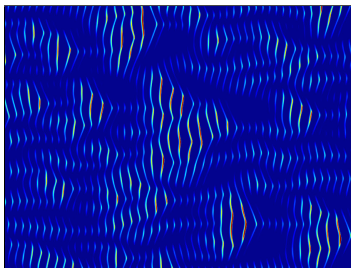
Ecological Dynamics

Ecological networks (2 / 2)

Dr. Tarik C. Gouhier
<tarik.gouhier@gmail.com>

Northeastern University
<http://blackboard.neu.edu>

March 26, 2015



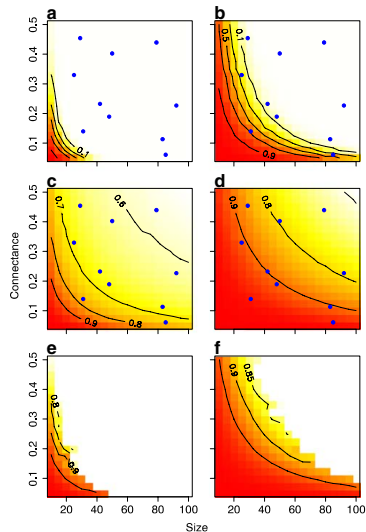
Network complexity, predictability and stability

We have seen that the topological features of food webs can provide important insights about their stability and persistence.

However, we still do not know whether these structural features can allow us to understand and predict the dynamical properties of food webs.

Overall, our goal is to determine (i) the features of natural food webs that promote their stability and (ii) whether the parts (e.g., pairs of species) can be used to predict the whole (food web networks).

Structural stabilization of food webs



May (1972) assembled food webs by randomly selecting the interaction coefficients α_{ij} and showed that complexity generally bets instability.

Allesina and Pascual (2008) used the same approach but constrained the structure of food webs by only allowing predator-prey interactions such that: $\text{sign}(\alpha_{ij}) = -\text{sign}(\alpha_{ji})$.

Incorporating only predator-prey interactions stabilizes food webs across a range of complexity (S) and connectance (C) values.

Does structure determine behavior?

To determine whether food web structure can predict the effects of perturbations applied to individual species, Novak et al. (2011) used a method called loop analysis (Levins, 1974) to analyze a food web model:

$$\frac{dN_1}{dt} = f_i(N_1, N_2, \dots, N_S)$$

Where the f_i can represent any functional relationship between focal species i and the rest of the species in the community.

This system can be described by generating an **community matrix** A_{ij} such that:

$$A_{ij} = \frac{\partial f_i}{\partial N_j}$$

Does structure determine behavior?

Where $\frac{\partial f_i}{\partial N_j}$ is the partial derivative of f_i with respect to the abundance of each species j .

The response of each species i to a **press perturbation** can then be determined by inverting the negative of \mathbf{A} to determine the effect of adding a small number of individuals I_j to species j :

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

Here, $-(\mathbf{A}^{-1})_{ij}$ measures all the direct and indirect effects of species j on focal species i .

The sign structure of $-(\mathbf{A}^{-1})_{ij}$ can thus be used to predict the net effect of perturbations on each species in the food web.

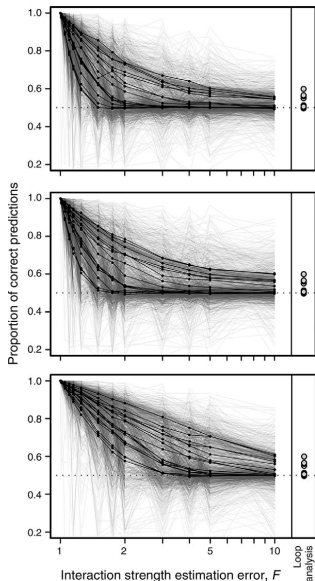
Does structure determine behavior?

Novak et al. (2011) used this approach to determine whether knowledge of who eats whom (presence or absence of interaction) vs. imperfect information regarding the strength of species interaction could predict the effect of perturbations.

Specifically, they simulated 17 empirical food webs and thousands of food webs based with different levels of complexity S and connectance C via the nice model.

They then predicted the effect of perturbations using realistic levels of error observed in the measurement of species interactions in the field.

Effects of perturbations in empirical food webs

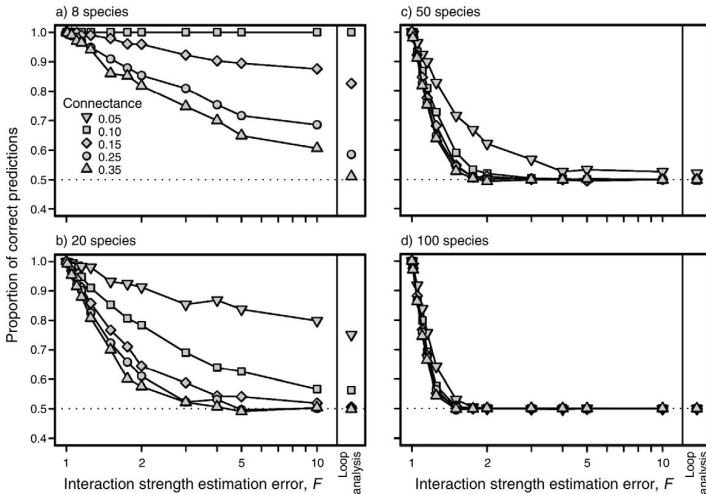


Predictability decreases quickly with increasing observational error about species interaction strength.

The presence vs. absence of interactions has almost no predictive power in 17 empirical food webs.

This occurs all food webs whether imperfect information applies to all, or only weak or strong species interactions.

Effects of perturbations in model food webs



The same patterns hold for niche model food webs, especially when complexity and connectance are high.

Conclusion

Overall, these results are pretty damning: accurate prediction requires good estimates of all species interactions, all $S!$ of them.

This suggests that understanding detailed information about individual species interactions is both **necessary and sufficient** to predict the whole.

Hence, classical reductionist approaches can be used to understand complex and interconnected ecosystems.

From structure to dynamics

Remembers that Novak et al. (2011) assumed that the interaction strengths came from a beta distribution.

Would adding more realistic biological constraints on the strength of species interactions improve predictive power?

Berlow et al. (2009) used a widely observed allometric scaling relationship between body mass and metabolic rate to constrain the strength of species interactions within an **allometric trophic network** model.

From structure to dynamics

Berlow et al. (2009) simulated the dynamics of the following network model containing basal species R_i and consumer species C_i :

$$\begin{aligned}\frac{dR_i}{dt} &= r_i G_i(N) R_i - x_i R_i - \sum_{i \in C} x_i y C_j F_{ji} / e_{ji} \\ \frac{dC_i}{dt} &= -x_i C_i + \sum_{i \in C} x_i y C_i F_{ij} - \sum_{i \in C} x_i y C_j F_{ji} / e_{ji}\end{aligned}$$

Where $x_i = \frac{a_x}{a_r} \left(\frac{m_i}{m_b} \right)^{-1/4}$ is the metabolic rate which depends on allometric constants a_x and a_r and the mass m_i of focal species i and the mass m_b of basal resource b .

From structure to dynamics

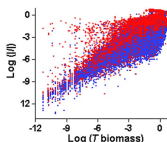
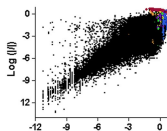
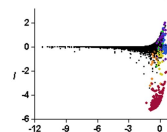
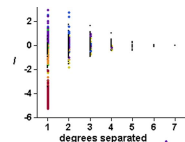
F_{ij} is the fraction of the maximum consumption rate species i can reach by feeding on species j , y is the maximum consumption rate and e_{ji} is the assimilation efficiency of species j when feeding on species i .

In addition, the model assumes that the basal resources compete for two types of nutrients and that the food web is structured based on the niche model.

Using this approach, Berlow et al. (2009) determined the effect of removing each species R one at a time.

They then measured their ability to predict the effect of the species removal R on each target species T by averaging the following interaction strength $I = C_T^+ - C_T^-$ across all T species.

Allometric scaling and predictive power

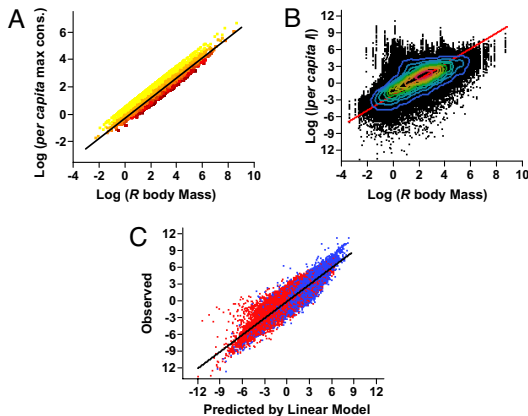


The magnitude and sign of interaction I is driven by C_T^+ and R .

A multiple regression of I against C_T^+ and R yields a good fit ($R^2 = 0.66$).

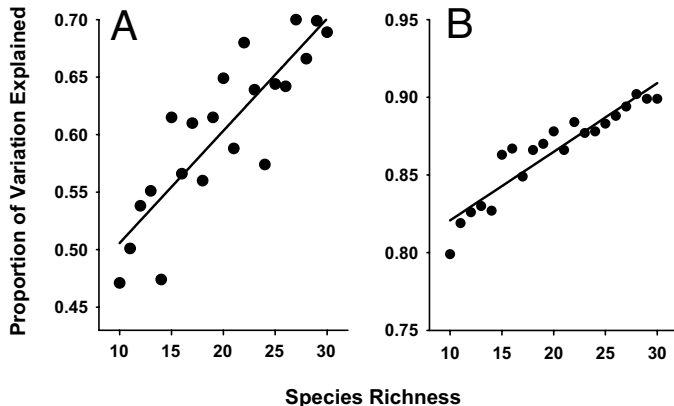
This indicates that we can predict the effect of removing species R on target species T based on their abundances prior to the removal.

Allometric scaling and predictive power



The simple statistical model does an admirable job of predicting the effects of species deletions averaged across all species in the food web.

Allometric scaling and predictive power



This is probably the most interesting result from the study: predictive power **increases** with complexity!

Conclusion

Overall, the results of Berlow et al. (2009) suggest that regardless of the complexity of the food web, accurate prediction is achievable as long as the species interactions are constrained by realistic allometric scaling laws.

Reductionist approaches can thus be used to predict the response of complex food webs without needing to estimate the strength of each pair-wise species interaction.

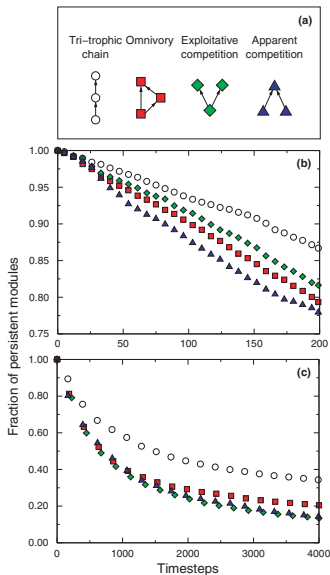
This represents a triumph of **bioenergetic food web** perspective over the **descriptive** and **interaction** perspectives used by Novak et al. (2011).

From community modules to full food webs?

Since food webs are composed of community modules, it may be possible to understand the aggregate behavior of the system based on that of each module.

Stouffer and Bascompte (2010) used the allometric trophic model developed by Berlow et al. (2009) to determine whether the stability of community modules in isolation could be used to predict their stability within a food web.

Persistence of community modules in isolation

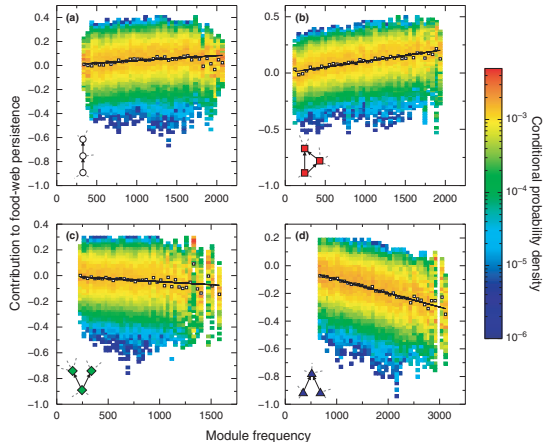


The persistence of each module decreases over time.

Food chains persist more than all other community modules.

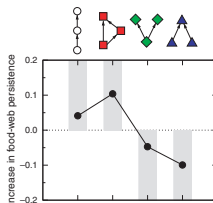
Competitive modules (exploitative and apparent) appear to persist less.

Persistence of community modules within food webs



Increasing the frequency of food chains or omnivory loops promotes persistence while increasing the frequency of competitive modules reduces persistence.

Conclusion



Overall, the results demonstrate that the persistence of modules in isolation is not a good predictor of their effect on persistence when incorporated into full food webs.

Intriguingly, the modules that promote food web persistence the most are found more frequently in empirical food webs, suggesting a link between module and food web stability.

Hence, this suggests that we need to shift from reductionism to **organicism** because knowledge of the whole is necessary to understand the parts and vice versa.

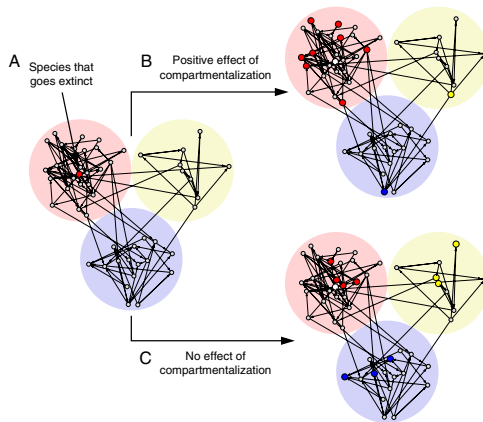
The complexity-stability debate

So far, we have identified structural features such as connectance that promote the persistence of static food webs.

However, there is a need to go beyond static food webs to understand how structure and dynamics interact to explain the persistence of complex empirical food webs.

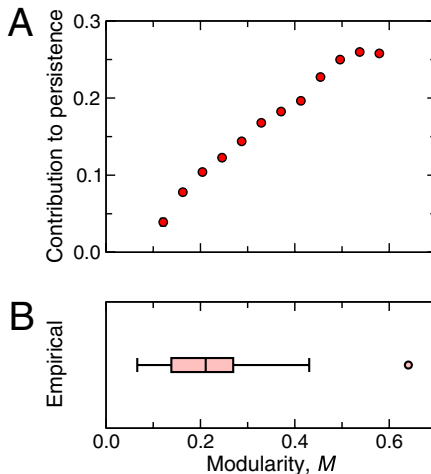
Stouffer and Bascompte (2011) used the allometric trophic network model described previously to investigate how **modularity**, defined as the tendency of species to interact more with a subset of the community, affects stability and persistence.

Modularity and stability



The extinction of the species in red will either be localized within a compartment when modularity is high or propagate across the entire food web if modularity is low.

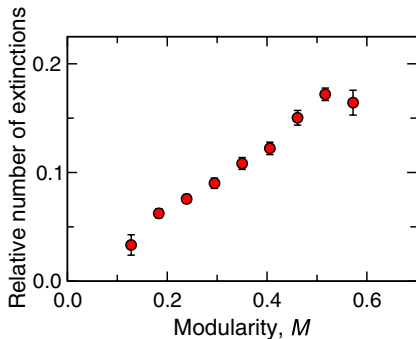
Modularity and stability



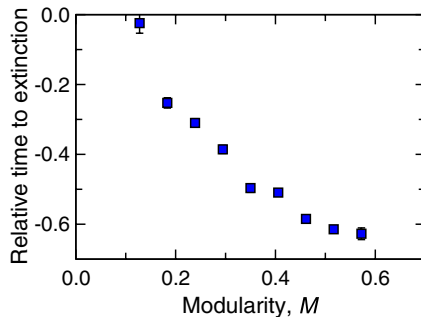
Increasing modularity promotes persistence and reduce extinction risk across the **entire food web**.

Modularity and stability

A

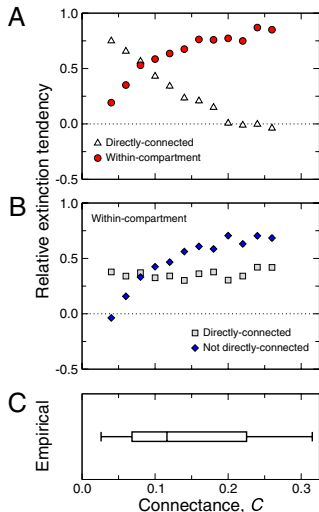


B



Increasing modularity reduces persistence and promotes extinction risk **within compartments**.

Modularity and stability



Connectance increases extinction risk within compartments.

The increase in within-compartment extinction is largely driven by species that are not directly connected to the deleted species.

Hence, although connectance promotes persistence in static food webs, it is associated with reduced persistence in dynamic food webs.

Complexity, predictability and stability of ecosystems

We have reviewed a suite of different approaches for studying complex ecosystems.

The general consensus is that incorporating biological realism such as allometric scaling laws can promote predictive power.

Furthermore, the inclusion of biological realism can help resolve May (1972)'s paradox by explaining why many natural ecosystems are both complex and stable.

This is an emerging field and there is still much work needed to integrate food web network theory and spatial community ecology in order to understand Earth's complex and interconnected ecosystems.

References

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