Linking Local Decisions with Global Outcomes in Networks: Case Studies in Behavior and Population Health

Nina Fefferman, Ph.D.

University of Tennessee, Knoxville NIMBioS/Ecology & Evolutionary Bio/ Math



Self-Organizing Networks

Emerge from Individual behavioral choices

- Not merely "emergent"
- Choices reflect decisions based on the network



Make Friends with Popular People



Emergent and Self-Organizing

Self-Organizing Animal Social Networks

Emerge from individual behavioral choices that depend on the behaviors of others

- Proximity
- Grooming
- Aggression
- Mating
- Communicating (harder to tell)



Individual Benefits from Being in a Group

Group Success

Benefit to the individual, but achieved collaboratively

Diffusion of risk from predators



- Increased foraging success
- Better engineering



From telegraph.co.uk

Individual Benefits from Being in a Network

Very cool studies have looked at evolutionary fitness associated with social network position

- Can genes determine position in a network?
- Do particular positions lead to better survival/more

reproduction?

These focus on direct, individual fitness outcomes



From sci-news.com

Individual Costs to Being in a Group/Network

Group Participation is not without costs

- Attract predators
- Competition for food/mates
- Disease transmission



Group Benefits, Individual Success

This sets up a system of feedback control

- Individual-scale self-organization
- Direct and Indirect fitness components
- Selection includes group benefits and costs
- Individuals pass on their genes or not



Bio Language: Multilevel Selection Math Language: Multiscale Feedback Control



Reproduced from Hock, Ng and Fefferman, 2010

To explore, we build a mathematical abstraction and use it as a computational experimental system

Assumption: Individuals make genetically determined "selfish" social affiliation choices (with no regard for group-level effects)

Initial hypothetical proxies of 3 measurements of social status from social network theory:

- Degree non-transitive dominance hierarchy
- Closeness genetic relatedness
- Betweenness much more complicated, assumed much harder to detect

Centrality has useful built-in features:

	Individual Outcome	Global Outcome
degree	$D(v_i) = \frac{d_{in}(v_i)}{n-1}$	$\frac{\sum_{i=1}^{n} (D^* - d_{in}(v_i))}{(n-1)(n-2)}$
closeness	$C(v_i) = \frac{n-1}{\sum_{j \neq i} d(v_i, v_j)}$	$\frac{\sum_{i=1}^{n} C(v_i)}{(n-1)(n-2)}$
betweenness	$B(v_i) = \frac{2\text{count}(v_i)}{(n-1)(n-2)}$	$\frac{\sum_{i=1}^{n} B(v_i)}{(n-1)(n-2)}$

Experimental setup:



- Initialize a digraph with *n* vertices
- Randomly generate arcs such that each vertex has out-degree = 5
- Then we iterate the following steps
 - Compute the 3 centrality measures for all of the vertices and for the entire network
 - In each step, each vertex drops two (how on next slide) of its existing out-neighbors and replaces them with two new ones

3 Different types of Populations – How to choose which social contacts to drop

• Each vertex drops two of its existing out-neighbors and replaces them with two new ones

All individuals in a population use the same measure (Degree, Closeness or Betweenness) to evaluate others

Each individual drops the two out arcs to the two affiliates with the worst centrality measure (among the five neighbors) and picks up two new ones (ratios are arbitrary, results are robust)

In all types of populations, we record all of the centrality measures for each individual and for the entire network over time

Unimportant Note: Not Just a Model System

A bunch of real-world human networks are actually Centrality self-organizing:



How to choose which social contacts to pick up

Three different ways:

Incomplete knowledge – individuals know centrality of only their current contacts, so two new contacts are chosen at random from all the rest

Complete knowledge – individuals know the centrality measure of everyone and choose the two best

Zero Knowledge – individuals have no centrality measure preference – so they drop two connections at random (and then add back two new ones at random)

Note: We don't need to be able to calculate centrality to have good proximate ways to estimate it

The evolutionary interpretation of the levels of knowledge

Zero-knowledge : before to the evolution of individual social choice **or** individuals are terrible at evaluating each other's status (no good proximate mechanism)

Complete-knowledge : social choice in smaller populations where you can evaluate everyone

Incomplete-knowledge : social choice in larger populations where you can only evaluate your friends

Convergence!



Iteration 1



Iteration 50



Iteration 100



Result: Different Individual Strategies Work to Accomplish Different Group Outcomes

 $D ? B > C > R \qquad R > C > B > D \qquad R > C > B > D$



Already gives us some insight into evolutionary pressures on self-organizing social behaviors Discussed in Fefferman and Ng, 2007a and Hock and Fefferman 2011, and 2012

Good abstract experimental system: separation in success across metrics and among populations with these traits





Reproduced from Fefferman and Ng, 2007

And the stability and success under Closeness?



Iterations x10

Reproduced from Fefferman and Ng, 2007

And the stability and success under Betweenness?

Measured Metric is Betweenness





Reproduced from Fefferman and Ng, 2007

Selection and Population Size



Already gives us some insight into evolutionary pressures on self-organizing social behaviors in populations of different sizes!

Reproduced from Fefferman and Ng, 2007

Λ

<

 $\langle \rangle$

R

B Inc

C Inc

D Inc

B Com

C Com

D Com

Can this happen?

We would need at least one of the following:

- (1) Neutral outcomes no net impact
- (2) Individuals do well by choosing things that accidentally are best for the group
- (3) Individuals may or may not benefit, but any costs are recouped by the distributed effects of group benefits

Do any of these 3 things happen?

In math language: Do global feedback rules to local decisions prohibit this type of emergence?

In bio language: Can this type of system evolve by natural selection?

Answers Come from Studying Rule-Breakers

How do individuals do if they follow the Degree self-organizing rule or not?



Size is Scaled by Degree

Reproduced from Hock and Fefferman, 2011

Answer for Degree: Neutral



Individuals do just as well if they do or do not participate in the self-organizing rule of Degree

HOWEVER, rule-breakers change overall group organization *even though* individual values don't change *(means evolutionary incentive to participate)*

Reproduced from Hock and Fefferman, 2011

What About Following the Betweenness Self-Organizing Rule?



Size is Scaled by Betweenness

Reproduced from Hock and Fefferman, 2011.

Answer for Betweenness: Net Benefit



Small numbers of rule breakers do better, large numbers of rule breakers mean only some do better

Consistent with the previous group-level analyses, with more rule-breakers, the whole population did better – evolution of this system may be unstable

Reproduced from Hock and Fefferman, 2011.

What have we built? Not a model of a real system

Experimental system with nice properties

- Self-organizing behaviors
- Individual benefits
- Group benefits

Global outcomes provide mechanism of control on evolution of social traits

- Insights into organizational success and population size
- Evolution of cooperation

Quantitative predictions about stability of self-organizing systems

Group Success May Not Be Our Network-Level Outcome – Lessens in Epidemiology!

Simulated Disease Process (SEIIS) on All Population Types:



Reproduced from Fefferman & Ng 2007

A Few Quick Cool Things I Won't Explain Today:

Can be found in Fefferman and Ng, 2007; Hock and Fefferman, 2011.

Super-spreaders aren't always high degree individuals in networks with ongoing selforganization!

Computational experiments on coupled stochastic processes are tricky – use a complete graph as a way to cheat the number of model realizations needed for network evolution AND epidemic spread

Different self-organizing strategies increase population robustness against disease at different probabilities of per-contact transmission

Increased network centrality doesn't always correlate with increased disease burden

One Thing I Will Talk About Quickly:

Details in Fefferman and Ng, 2007

Ongoing self-organized rewiring dynamics were *protective* against disease

Disease on Self-Organizing Networks

		B-population		C-population		D-population	
	3-Way Test	Dynamic	Static	Dynamic	Static	Dynamic	Static
В	Dynamic [¶]	B static $>$ B dynamic [†]		<*	<*	>	>*
С		$C \text{ static} > C \text{ dynamic}^{\dagger}$		>*	>*		
D	Static ¹	Static ¹				D static > D dynamic [†]	
Overall: Dynamic C>B>D; Static C>B>D							

Reproduced from Fefferman and Ng, 2007b

Finally! We discovered computationally something we can prove analytically!

I'm actually not going to go through the proof

The Intuition for how

- Instead of estimating numbers of infections, focus on threshold in transmissibility that implies transmission will occur on the current network state
- Calculate limit of recurrence relation of shifting states
- Compare boundaries of that threshold for static and dynamic network recurrences



These systems are analytically challenging (even in the simple, deterministic cases)

- Bi-directionally coupled
- Coupling occurs at multiple scales
- Scale of coupling can (and usually is) asymmetric
- Frequently discrete in individual action, though continuous in global dynamics

When should we even bother looking for analytic approximations?

> Can we reduce the dynamics or shift the outcome variable to something with a well-defined recurrence relation?

- Is temporal order critical to individual dynamics?
- Can we approximate the global behavior without finding a good approximation for individual dynamics under any circumstances?

More Importantly:

There are reasons we can discuss analytic solutions for anything about this:

- We constructed the simulation to be a mathematically controllable abstraction
- It has minimal complexity for the features we need
- The observed behaviors come from single differences in action/assumption

Potential Recommendation for Studying Self-Organization (definitely not for everyone or every problem)

We all have a tendency to model actual biological systems

Instead, sometimes we might want to try modeling the simplest systems with isolated, abstract behaviors in mathematically controllable ways and *then* gradually put back the realism as we need it to gain further insight

Where some of these things (and more on this topic) are published:

- Brooks. H.Z., M.E. Hohn, C. Price, A.E. Radunskaya, S.S. Sindi, N.D. Williams, S.N. Wilson, N.H. Fefferman. 2018. Springer.
- Williams, N.D., H.Z. Brooks, M.E. Hohn, C. R. Price, A.E. Radunskaya, S.S. Sindi, S.N. Wilson, and N. H. Fefferman. 2018. Springer.
- Gallos, L., and N.H. Fefferman. 2015. *PLoS One.*
- Greening, B. and N.H. Fefferman. 2014. *Nature Sci Rep.*
- ► Hock, K. and N.H. Fefferman. 2012. *Ecological Complexity*.
- Hock, K. and N.H. Fefferman. 2011. *PLoS One.*
- Hock, K. and N.H. Fefferman. 2011. Ann Zoo Fen.
- ► Hock, K., K.L. Ng, and N.H. Fefferman. 2010. *PLoS One.*
- Fefferman, N.H. and K.L. Ng. 2007. *Physical Review E*.
- Fefferman, N.H. and K.L Ng. 2007. Ann Zoo Fen.

Talented Researchers of the Fefferman Lab:



Post docs: Dr. Erick Chastain, Dr. Jing Jiao (starting soon!), Dr. Kellen Myers, Dr. Nourridine Siewe, Dr. Gonzalo Suarez, and Dr. Oyita Udiani (Former post docs pictured because their work was presented: Dr. Karlo Hock and Dr. Kah Loon Ng)

Grad Students: J. Beck, J. DeSalu, A. Redere

Funders to the lab: NSF, NIH, DHS, DoD, USDA, USFWS