Collective Behavior of Many Species Ecosystems

Davneet Kaur

May 8, 2017

Abstract

Ecoevolutionary dynamics have long been of interest. However, our understanding of diverse systems has largely been based off of induction of our understanding of simpler systems with few species. This approach fails to reveal many important emergent phenomena. In this paper, I will first discuss two complementary ways of breaking down and understanding diverse complex systems. That is, analyzing the system in terms of regimes in phase space and in terms of the MacArthur Competition Equations. Following this discussion, I will briefly outline two recent works. In the first paper, the authors analytically solve the MacArthur Model in the high-diversity limit and reveals the presence of a phase where the immediate environment of individuals becomes fully decoupled from the outside world. In the second paper, the authors propose and experimentally test an assembly rule for predicting survival in multi-species competitions from the outcomes of pairwise competitions. I will conclude with a summary of the material and some closing thoughts.

Contents

1. Introduction

1.1 The Whole is Greater Than The Sum of Its Parts

Many complex behaviors can manifest in minimalistic models of complicated systems. These models, in addition to providing technical simplifications, act as tools for identifying and understanding the leading contributors to the dynamics of a system. However, it's important to identify where the intuitions built on a simplified scenario break down and fail to reflect scientific observations. As we've learnt from multiple disciplines, and particularly well from the likes of ecology and theoretical physics, the whole is greater than the sum of its parts. Novel and non-intuitive collective behaviors or community level effects arise in systems with increased complexity and often aren't predicted by their more tractable minimalistic models (N=2 =/not extendable/=> N -> infinity.) It has become increasingly important to develop a theoretical framework capable of describing complex and diverse communities to better supplement and further research in concerned fields, such as, in the study of microbiota. There is potential for such a framework to be developed from the statistical physics of disordered systems.

1.2 Importance of Diversity in Diverse Ecosystem

I'm keenly interested in diverse ecosystems and their ecoevolutionary dynamics. Though ecoevolutionary dynamics have long been of interest to humanity in general (predating formal science), our understanding of diverse systems (large N) has largely been based off of induction of our understanding of simpler systems with few species (small N) to large N. This approach fails to reveal many interesting phenomena. For instance, a recent simulation-based study of an ecosystem with just ten different groups of resources exhibited a surprising regime shift effect. It was observed that community-community introduction (coalescence) would produce an effective cohesion even without cooperative interactions between its members. This effect arises purely as a consequence of the environmental feedback of the resource utilization. The study demonstrated that the ability of an individual species to survive a coalescence event was a measure of the community-level fitness of its native community rather than the intrinsic performance of the species itself [1]. Complex microbial communities in nature have even larger numbers of metabolites, of the order $N \simeq 100$ [2,3]. Hence, high-diversity communities can contain qualitatively novel and non-intuitive regimes. Furthermore, diversity demonstrably strengthens a community's ability to withstand environmental variation [4,7].

1.3 Broader Relevance and Personal Interest

The resilience and stability of diverse ecosystems are particularly important properties that are demonstrably dependent on (and strengthened by) the diversity of the system [4]. Given humanity's ever expanding influence on ecosystems across the globe (and eventually beyond), it's important that we understand our impact on the resilience, stability and sustainability of these complex systems and control and counter the damage we inflict on them. Regime shifts in ecosystems as a consequence of human activities are increasingly common. These shifts are capable of eroding resilience through, for example, resource exploitation, targeted selection of species (e.g., hunting), pollution, possible climatic impact, etc. Biodiversity acts as a buffer to this erosion by playing a strong role in the renewal and reorganization of ecosystems after such disturbances. In other words, biodiversity plays a significant stabilizing effect for ecosystems [5]. It helps sustain desired states of ecosystem dynamics in the face of uncertainty and surprise [6]. It is also important to uncover strategies to revert degraded ecosystems back into desirable states or transform them into new and preferable configurations.

In this paper, I will first discuss two complementary ways of understanding complex systems as more manageable fragments. That is, analyzing the system in terms of regimes in phase space [4] (or community level states) versus in terms of individual species competition equations [7] (MacArthur Model). Following this discussion, I will briefly outline two recent works. The first analytically solves the MacArthur Model under certain assumptions [8]. The second proposes and experimentally tests an assembly rule for predicting survival in multi-species competitions from the outcomes of pairwise competitions. I will then proceed to summarize and discuss the material with some closing thoughts.

2. Methods of Analysis

It is important to define our tools for mathematical analysis in biologically significant terms. The definition of resilience is one such example that has changed its mathematical meaning to better represent the biological process and better describe the dynamics of perturbed system.

2.1 Resilience and Stability in Phase Space

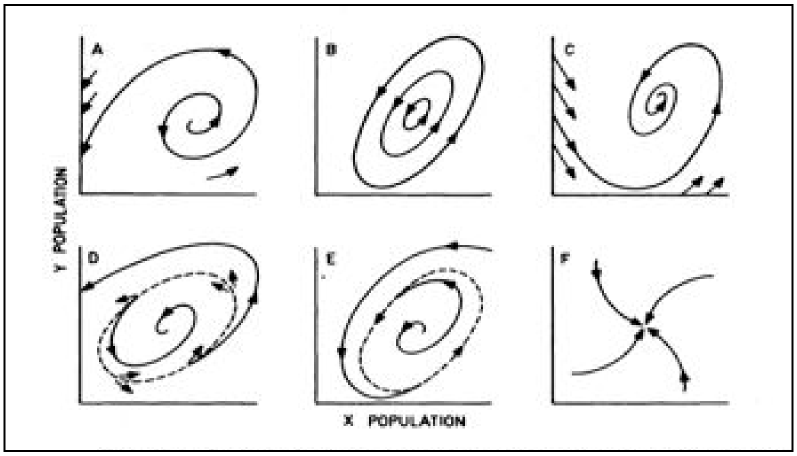
When we talk about resilience, we're talking about a system's response to disturbances or fluctuations in phase space. The system can respond in many ways, a few of which are depicted in Fig.1. An earlier definition of resilience was what is now known as engineering resilience, which is simply the speed with which a system returns to equilibrium. This is what MacArthur refers to as resilience in [7].

In his seminal paper, Holling defined ecosystem resilience [4] as,

> *"the magnitude of disturbance that a system can experience before it shifts into a different state (stability domain) with different controls on structure and function."*

An updated definition of resilience from [5] adapted from [9] is,

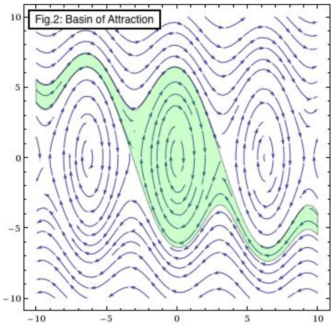
> *"the capacity of a system to absorb disturbance and reorganize while undergoing change so as to retain essentially the same function, structure, identity, and feedbacks."*



[4]

Fig. 1: The System Dynamics in Phase Planes: The system can behave in a number of possible ways in phase space, (A) Unstable Equilibrium: Fluctuations gradually increase in amplitude. (B) Neutrally Stable Cycles: Given any starting point eventually return to it. (C) Stable Equilibrium: All possible trajectories spiral into an equilibrium. (D) Domain of Attraction: All trajectories spiral in within defined (dotted) region and fluctuations gradually increase in amplitude outside defined region. (E) Stable Limit Cycle: Fluctuations gradually increase in amplitude inside defined (dotted) region and all trajectories spiral in outside defined region. (F) Stable Node: No oscillations and with trajectories approaching the node monotonically.

2.1.1 Concept Demonstrating Example



I'd like to discuss a concept demonstrating example of regime shifts: lake phosphorus cycles. Lake phosphorus cycles exhibit multiple regimes, but two are particularly noteworthy because of their favorability and unfavorability to the people who are a part of the lake's ecosystem: clear-water and turbid-water regimes. Research on lake phosphorus cycles has revealed techniques of undoing degradation and reverting the ecosystem back to a desirable regime. We are essentially moving between different basins of attraction in phase space. The basin of attraction for a point at the center of Fig. 2, for example, is depicted as the highlighted portion (an example taken from Mathematica stack exchange.)

Favorable Regime: In the clear-water regime, phosphorus inputs, phytoplankton biomass, and recycling of phosphorus from sediments are relatively low [10]. This regime is favorable as it provides higher ecosystem services with extensive beds of higher aquatic plants (macrophytes), which stabilize sediments and reduce the recycling of phosphorus to phytoplankton [11,12].

Unfavorable Regime: In the turbid-water regime, the above discussed concentrations are relatively high. This regime is unfavorable as it provides lower ecosystem services with high levels of toxicity and low concentrations of oxygen [10].

Fluctuation: High Phosphorus Inputs: Sediment-stabilizing macrophyte beds may erode when high phosphorus inputs stimulate phytoplankton growth. An increase in the abundance of bottom-feeding fishes with nutrient enrichment from phytoplankton growth damages the macrophytes. This in turn causes turbidity by resuspending sediment.

Type of Response to Fluctuations: Loss of the macrophytes results in easy resuspension of sediments by waves and consequent rapid recycling of phosphorus from sediments maintains the turbid regime.

Reversion to Original Regime: In order for the system to return to the clear-water regime, we must first lower phosphorus inputs. However, the turbid state can still persist. If phosphorus levels are low enough, the system can be perturbed back to the clear-water state by the removal of fish. This removal stimulates macrophyte regrowth and stabilizes the cycling of both sediments and phosphorus, suppressing turbidity.

2.2 Resource Competition Models (Classical MacArthur Model)

The Classical MacArthur Model of Resource Consumption [7] has become a paramount body of work that we continue to draw from and build on today. It seems that MacArthur's purpose in proposing this minimalistic model was to construct an ecological counterpart to the minimum principle of a physical system at static equilibrium conditions, namely to locationally configure itself such that its potential energy is minimized. Hence, he defines Q, a quadratic expression that is minimized by competition for certain sets of competition equations. This expression provides an important picture for intuitive understanding of ecosystem equilibrium states and their stability.

2.2.1 Introduction

MacArthur wrote a set of competition equations for the population sizes (in grams) of *n* species:

$$\frac{1}{X_i}\frac{dX_i}{dt} = C_i\left[\mathscr{K}_i - \sum_{j=1}^{n} \alpha_{ij}X_j\right] \qquad i = 1,\ldots, n,$$

where all $\mathscr{K}$ (surplus grams of resources used towards growth) and C (constant of proportionality governing biochemical conversion of grams of resource into grams of *X,* the population size) are positive and all α (harvesting ability) are nonnegative. Each equation for population size includes a term for species *i*'s own consumption needs and a term establishing its interaction/competition with other species to obtain resources. This is a simplified model that does not include higher order and higher derivative terms which would correspond to 3-and-above species interactions, effects of seasonality, effects of patchy environments, age distributions, and so on. Also, these equation lack the more elaborate form needed to account for the dynamics of competition which usually require non-equilibrium conditions. However, this equation is useful near equilibrium.

2.2.2 Competition for Non-interacting Resources

Like before, we can define the species' consumption:

$$\frac{1}{X_i}\frac{dX_i}{dt} = C_i\left[\sum_k a_{ik}w_k R_k - T_i\right],$$

where different resources (with abundance, *R*) are now denoted with subscript '*k*', ω_k is the weight of resource *k* in grams, and T_i is the threshold resource requirement of species *i*.

We define the resource supply by:

$$\frac{1}{R_k}\frac{dR_k}{dt} = \frac{r_k}{K_k}\{K_k - R_k\} - \sum_j a_{jk}X_j = \frac{r_k}{K_k}\left[K_k - \sum_j a_{jk}\frac{K_k}{r_k}X_j - R_k\right].$$

where K_k and r_k are positive constants. MacArthur assumed that this model applies to near-equilibrium states of the ecosystem populations, and hence it's safe to assume that the resource supply equations are at a stationary state. This gives the resources level at equilibrium renewal,

$$R_k = K_k - \sum_j a_{jk} \frac{K_k}{r_k} X_j$$

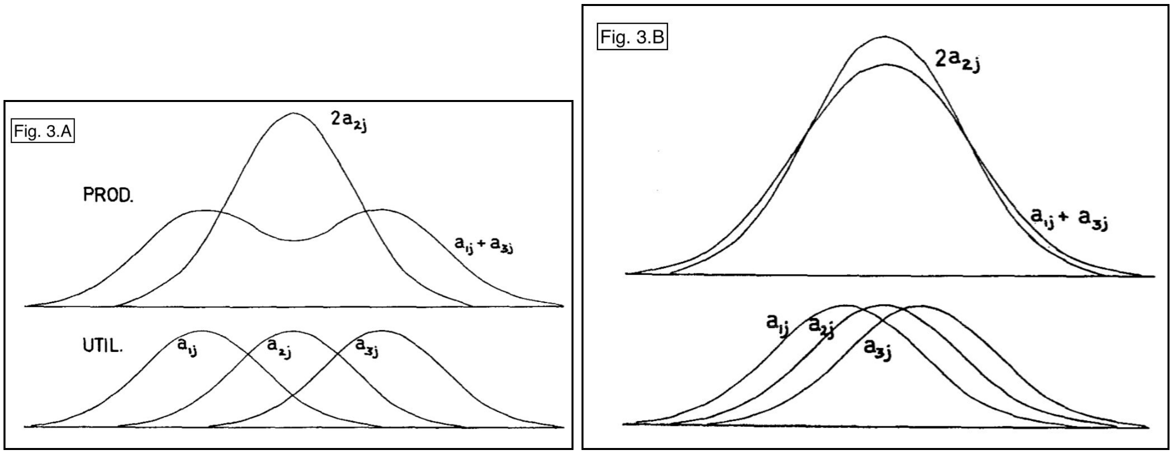
Combining this with the consumption equations at give consumption at equilibrium resource level,

$$\frac{1}{X_i} \frac{dX_i}{dt} = C_i \left[\left\{ \sum_k a_{ik} w_k K_k - T_i \right\} - \sum_j \left\{ \sum_k a_{ik} a_{jk} \frac{w_k K_k}{r_k} \right\} X_j \right].$$

For this system of equations and under the assumptions that (1) all species have the same threshold resource requirements $T_i = T$ and (2) the same total harvesting ability $\sum_j \alpha_{ij} = \alpha$, independent of i, our minimizable quadratic expression, Q is,

$$Q = \sum_k \frac{w_k K_k}{r_k} \left[\left(r_k - \frac{T r_k}{a w_k K_k} \right) - \sum_j a_{jk} X_j \right]^2$$

The system minimizes Q at equilibrium. Given this expression for Q with the above assumptions, we can now understand Q as the weighted (by *wK/r* terms) squared deviation of available production from the species' harvesting abilities. The problem then becomes one of finding the best fit for all the species' harvesting abilities to the available resource production as depicted in Fig. 3.



[7]

Fig 3. (A) The production curves illustrate the limitations of environmental variation within which the three depicted species will coexist. (B) Now the species are much more similar and tolerate less environmental variation than the species defined in A.

An important point here is that, as long as it reduces the value of Q, another species can be introduced to the system and this addition is favorable for the system's stability. That is, as long as it's improving the fit of the system, diversity is a favorable condition that improves the system's tolerance to environmental variation and hence its stability.

3. Recent Work

3.1 Analytic Solution to the MacArthur Model

In [8], the authors find an analytical solution to the MacArthur Model in the limit of a large number of species N (diverse). In this Letter, the authors adopt a statistical physics approach. The competing strategies for all species are drawn out of some ensemble. Each species has a 'foraging' strategy which is a binary vector (each value is either 1 with a probability p or 0) with each type of resource as a dimension. Each species is assigned a random cost reflecting its unique evolutionary history, physiology and lifestyle. A random cost or likelihood of success is argued to be a better null hypothesis than explicitly considering a single factor that would fail to encompass all of the above (and other) factors affecting success.

The authors observe a phase transition between two qualitatively distinct regimes. In the first regime, whose behavior is predicted by the low-dimensional case, changes of external conditions propagate to the immediate environment experienced by organisms. However, in the second regime, which emerges as a consequence of the large dimensionality of the system, the immediate environment of individuals becomes a collective property of the community. The immediate environment of individuals becomes disjoint from and unaffected by the outside world. Hence, this regime documents the emergence of a collective behavior brought on by the large dimensionality or diversity of the system.

The model considered here has no cooperative interactions built into it. The interactions were purely competitive: increasing the abundance of any one species hurts everyone else by taking a cut of their share and reducing each of their effective growth rate. Nevertheless, the authors observe emergent behavior, a strongly collective regime. There is an added layer of complexity that goes beyond the species-species interaction, yet also emerges from it in the high diversity limit.

3.2 Assembly Rules for Microbial Community Structure

The above models of microbial ecosystem structure use bottom-up approaches that assume that species interact in a pairwise manner. As we've seen, these models neglect higher order and derivative terms. However, when we consider diverse ecosystems, we need to consider that pair interactions may be modulated by the presence of additional species. This may significantly alter community structure and potentially be a major limitation to the predictive power of the above models. Moreover, they've rarely been directly tested experimentally. In the recent paper [13], the authors propose and experimentally test an assembly rule for predicting survival in multi-species competitions from the outcomes of pairwise competitions. The assembly rule is as follows:

> *In a multispecies competition, species that all coexist with each other in pairs will survive, whereas species that are excluded by any of the surviving species will go extinct.*

For the case of three-species competitions, they obtain an accuracy of ~90%. For higher values of N (=7 or 8), obtaining a similar degree of accuracy required incorporating the additional information from the outcomes of three-species competitions. These results demonstrate the predictive ability of the relatively easy to experimentally test bottom-up approach. There's a productive symbiosis between experiment and modeling that works well to understand and predict the behavior of realistic ecosystems. This makes this approach well suited to predict the response of communities to changing environments as well as designing ways of steering existing communities to more desirable states.

4. Summary and Discussion

All of the modeling methods considered here ignored spatial structure and focused on equilibrium states only. This made it possible to find an analytic solution of the MacArthur Model [8] and make predictions about the collective behavior of the system, like the presence of a phase transition. The key aspect that the authors didn't ignore and what enabled them to unveil another layer of complexity of the system is its diversity. To me, this work not only highlights the promise of applying statistical physics to gain insight into the non-intuitive behavior of complex systems, but also emphasizes the importance of tinkering and toying with well understood systems in new ways. Proceeding from here, the use of techniques of out-of-equilibrium statistical physics of disordered systems to seek insight into dynamical behavior of diverse ecosystems is probably a promising avenue of research. Also, we've seen the great predictive power of an effective feedback between experiment and modeling. This approach is uniquely suited to understanding and predicting the behavior of real ecosystems.

5. References

[1] M. Tikhonov, Community-level cohesion without cooperation, eLife 5, e15747 (2016).
[2] M. A. Fischbach and J. Clardy, One pathway, many products, Nat. Chem. Biol. 3, 353 (2007).
[3] M. A. Fischbach and J. L. Sonnenburg, Eating for two: How metabolism establishes interspecies interactions in the gut, Cell Host Microbe 10, 336 (2011).
[4] C. S. Holling, Resilience and stability of ecological systems, Annu. Rev. Ecol. Syst. 4:1-23 (1973).
[5] C. Folke, S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C.S. Holling, Regime shifts, resilience, and biodiversity in ecosystem management, Annu. Rev. Ecol. Evol. Syst. 35:557–81 (2004).
[6] T. Elmqvist, C. Folke, M. Nystrom, G. Peterson, J. Bengtsson, et al., Response diversity and ecosystem resilience. Front. Ecol. Environ. 1:488–94 (2003).
[7] R. MacArthur, Species packing, and what interspecies competition minimizes, Proc. Natl. Acad. Sci. U.S.A. 64, 1369 (1969).
[8] M. Tikhonov and R. Monasson, Collective phase in resource competition in a highly diverse ecosystem, Phy. Rev. Lett. 118, 048103 (2017).
[9] B. H. Walker and J. A. Meyers, Thresholds in ecological and social-ecological systems: a developing database, Ecol. Soc. 9(2):3 (2004).
[10] V.H. Smith , Cultural eutrophication of inland, estuarine and coastal waters. In Successes, Limitations and Frontiers of Ecosystem Science, eds. ML Pace, PM Groffman, pp. 7–49. New York: Springer-Verlag (1998).
[11] E. Jeppesen, M. Sondergaard, M. Sondergaard and K. Christofferson, The Structuring role of submerged macrophytes in lakes. Berlin: Springer-Verlag (1998).
[12] M. Scheffer, The Ecology of Shallow Lakes. London: Chapman and Hall (1997).
[13] J. Friedman, L. M. Higgins and J. Gore, Community structure follows simple assembly rules in microbial microcosms, Nat. Eco. and Evol. 1, 0109 (2017).