

# **Analysis of Equilibrium Communities: An Account of a Yearlong Exploration and Meditation on Floral Diagrams**

**M.Sc. Thesis**

By  
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**DEPARTMENT OF BIOSCIENCES AND BIOMEDICAL  
ENGINEERING  
INDIAN INSTITUTE OF TECHNOLOGY INDORE  
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# **Analysis of Equilibrium Communities: An Account of a Yearlong Exploration and Meditation on Floral Diagrams**

**A THESIS**

*Submitted in partial fulfilment of the  
requirements for the award of the degree  
of*  
**Master of Science**

*by*  
**AMAN SAGARBHAI SHAH**



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INDIAN INSTITUTE OF TECHNOLOGY INDORE  
MAY 2025**





## INDIAN INSTITUTE OF TECHNOLOGY INDORE

### CANDIDATE'S DECLARATION

I hereby certify that the work which is being presented in the thesis entitled **Analysis of Equilibrium Communities: An Account of a Yearlong Exploration and Meditation on Floral Diagrams** in the partial fulfillment of the requirements for the award of the degree of **MASTER OF SCIENCE** and submitted in the **Department of Biosciences and Biomedical Engineering, Indian Institute of Technology Indore**, is an authentic record of my own work carried out during the time period from **July 2023 to May 2025** under the supervision of **Dr. Parimal Kar**, Head of the Department, Indian Institute of Technology Indore.

The matter presented in this thesis has not been submitted by me for the award of any other degree of this or any other institute.

Signature of the  
student (with date)

(Aman Sagarbhai Shah)

-----  
This is to certify that the above statement made by the candidate is correct to the best of my/our knowledge.

Signature of Supervisor of  
M.Sc. thesis (with date)  
(Dr. Parimal Kar)

-----  
Aman Sagarbhai Shah has successfully given his/her M.Sc. Oral Examination held on **MAY 7, 2025**.

Signature of Supervisor of MSc thesis

Date: 7/5/2025

Convener, DPGC

Date: 23-05-2025



## ACKNOWLEDGMENT

Is there a word to describe the kind of science I did during this Thesis period? How liberating I felt when I listened to Itai Yanai and Martin Lercher in their Night Science podcast! The word is “Night science.” In their wonderful article, they mentioned that night science is “where we explore the unstructured realm of possible hypothesis, of ideas not yet fully fleshed out (Yanai & Lercher, 2019).”

I feel that students should be given an equal chance to explore the field, engage in creative activity, and ponder on the data sets without any prior goals. This would sharpen not only their critical faculties but also their observational skills.

However, the problem is that this is rarely discussed, and most of the students are not aware of this possible direction. I did not know this beforehand when I chose to do my research independently. I was wandering here and there and later stumbled across the floral diagrams and those horrors of uncertainty! — things would have been much more productive during those initial days if I had known that what I was doing was night science—an exploration of ideas that are “not yet fully fleshed out.”

But be that as it may, wherever I am right now is not just an individual effort; it will never be. I am grateful to have an understanding supervisor and head of the department of BSBE, **Dr. Parimal Kar**, who allowed me to situate where I could explore, think, and ideate. I have done my best not to abuse the freedom I have gotten over the entire period of my thesis work, and I shall never try to do it beyond this period. Next, the person who weighed in during the tough time was **Dr. Sourav Chandra**, whose encouraging words really “mattered” to me then.

I am at a loss for words in order to describe **Dr. Amit Kumar**’s willingness to help me during the first year. He tried to help me as much as possible in different roles, from being a faculty advisor to a former HOD.

I have my thoughts for all the teachers of the world, especially of the BSBE department. Although I would not be regular in taking lectures, I was particularly enthused by **Dr. Ganti Murthy**'s lectures on research methodology, and for that, I distinctly acknowledge him here.

This cannot be complete without the mention of my parents. They have always supported me; if they do not understand what I am doing, they know whatever I and will do must be rightfully important to me, potentially to others, and, therefore, to themselves.

Among my friends, those who know me a little mercifully have never spoken about my work and understandably have given space to my moody behaviours.

And beyond the known, there is an unknown. I am most grateful for this part because that is where the mystery and the true freedom lie.



## Abstract

This thesis introduces “floral diagrams” as a novel conceptual framework to investigate equilibrium communities within an evolutionary ecology context. Inspired by nature’s continuous and stochastic processes, floral diagrams are graphical models governed by formal rules of intersection and endurance, representing the interplay of events, patterns, and randomness in ecological systems. In this framework, nodes symbolize environmental types, with leaves illustrating spaces of inter-trophic species coexistence, providing a lens to explore community resilience and balance across temporal, spatial, and phylogenetic scales. Concepts such as the “mirroring effect” and “reflective time” propose internal relatedness and global evolutionary dynamics among community members. Through a yearlong exploration, this work underscores the potential of floral diagrams to address scale-dependent patterns and unify ecological perspectives. Though theoretical, the framework establishes a foundation for future empirical research, offering innovative insights into the stability and evolvability of complex ecological systems.

**Keywords:** floral diagrams, equilibrium communities, evolutionary ecology, community resilience, scale-dependent patterns, mirroring effect, reflective time, stochastic process



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## **NOMENCLATURE**

PE system	Properties-Environmental type System
GE system	Gene-Environmental System
MGE systems	Multi-Gene-Environmental System

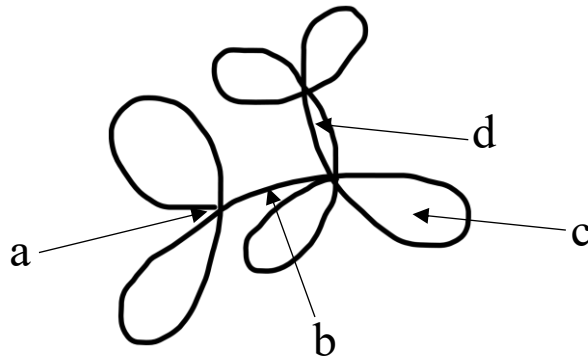




## Chapter 1

### Introduction to Floral Diagrams

Draw without lifting your pen in either a clockwise or anticlockwise direction; avoid intersecting self-loops; and intersect only to form new nodes. This basic command would generate what I call ‘floral diagrams’ (figure 1.).



**Figure 1. Floral diagram.** a) node created due to the intersection of indeterminate flow b) link connecting nodes continuously c) leaf of the node that is enduring d) a two-node loop

The scope of these floral diagrams, to my mind, looked so vast that I was caught up in contemplating its innumerable stretches. It was a matter of what it really represents, and with each representative supposition, the task of accounting and implicating its character differed. For example, if one argues that it talks about our thinking process, then how exactly? If it is the nature of how evolution works, then how exactly? What exactly it is and how to then explain it occupied me for this entire period, only later narrowing it down to two main possibilities. But before I go on, I shall mention the fundamental basis of the floral diagrams and the formal rules that they follow.

The passage of nature is such that the duration of an event penetrates into another duration of an event, giving us the continuous description of things or ‘entities’ that are ingressed in those events. In physics, discretization of the continuous field is sometimes essential in

order to grasp the character and relation of these specific entities. All that, however, is the abstraction of science. Indeed, on the face of this, the continuous passage of nature and time is one of the few reluctant agreements among physicists and philosophers.

“No thinker thinks twice.” When Alfred North Whitehead said this, he certainly pointed us towards this fact of nature. However, when a thinker notices relentless droplets of perspiration hanging on his nose, a certain peculiarity occurs to him. The droplets that were hanging a moment ago are still hanging on the nose. They are enduring at a certain position. The enduring entities, feelings, or patterns are in themselves an event, and to account for them, an idea of closure or intersection is direly needed. Without the intersection of the continuous flow, it would go to an infinite regress, and thereby, nothing would endure—the universe would not exist at all—which starkly contrasts our experience. This combination of the two features of nature, that is, the law of continuity and the idea of intersection, gave rise to these floral diagrams.

Randomness is another intrinsic feature of the diagram, which results in varied, unstructured diagrams, sometimes frequently overlapped and sometimes highly looped with the same no. of nodes, or sometimes both, but all the same, extremely dissimilar.

One particular organism that expresses such continuous outgrowing-like and stochastic features is fungi. Not only do they symbolize the continual development in nature, but the variation in their structures signifies the contingency or random fluctuations of nature, by nature, and for nature.

The formal rules that these diagrams follow is stated as follows:

- 1.) “Event is the unit of natural occurrence.” For any event to occur, by precluding the infinite regress of the indeterminate flow, the flow must pass through its precedent activities in an event called an ‘intersection.’
- 2.) The individualized event thereby has a) its aspects of patterns and b) an intersection.
- 3.) The corresponding enduring patterns of events never suffer any

further event of intersections other than the intersection that endures them.

- 4.) The stabilization of the event in the event of intersection determines the indeterminate flow but only within the spatial region of endurance.
- 5.) Events continuously form through such unique events of intersection.
- 6.) The time taken for the indeterminate flow to determine itself also determines the spatial region of endurance within which such determinacy lies.
- 7.) The time of endurance of the stabilized event must be way longer than the time of determinacy taken by the indeterminate flow.

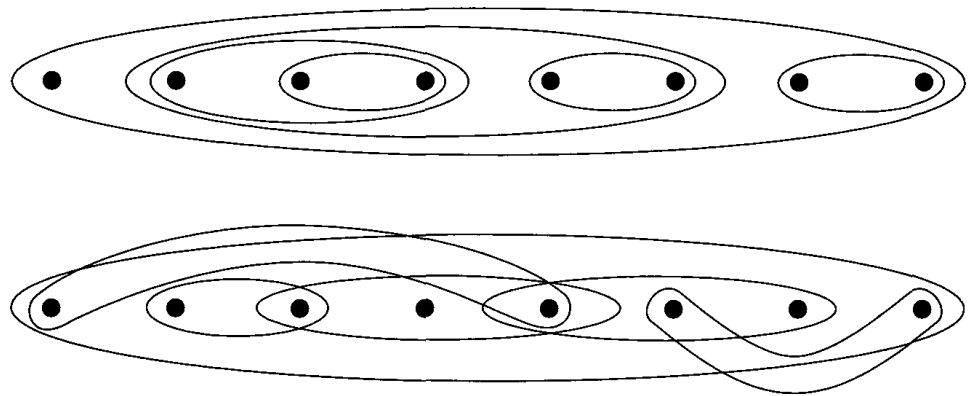
Although these rules look like an intellectual decoration, I would argue that they provide an abstract language that, once internalized, would stand alone like ideas that we can develop further for something completely different in some other context. This works because, after all, underneath all the abstract language lies the bedrock of innumerable possibilities! — human thought. Sub-contextual research on human thought is another motivation for the use of floral diagrams. And you'll see next that it taps into the fuzziness of things, sharply against the hierarchical structures that have dominated our scientific thinking over millennia. It is a burden I am taking to divorce myself from the existing frameworks whose achievements have brought mankind to the current stage of fruition.

### **1.1. Cyclicity vs Hierarchy**

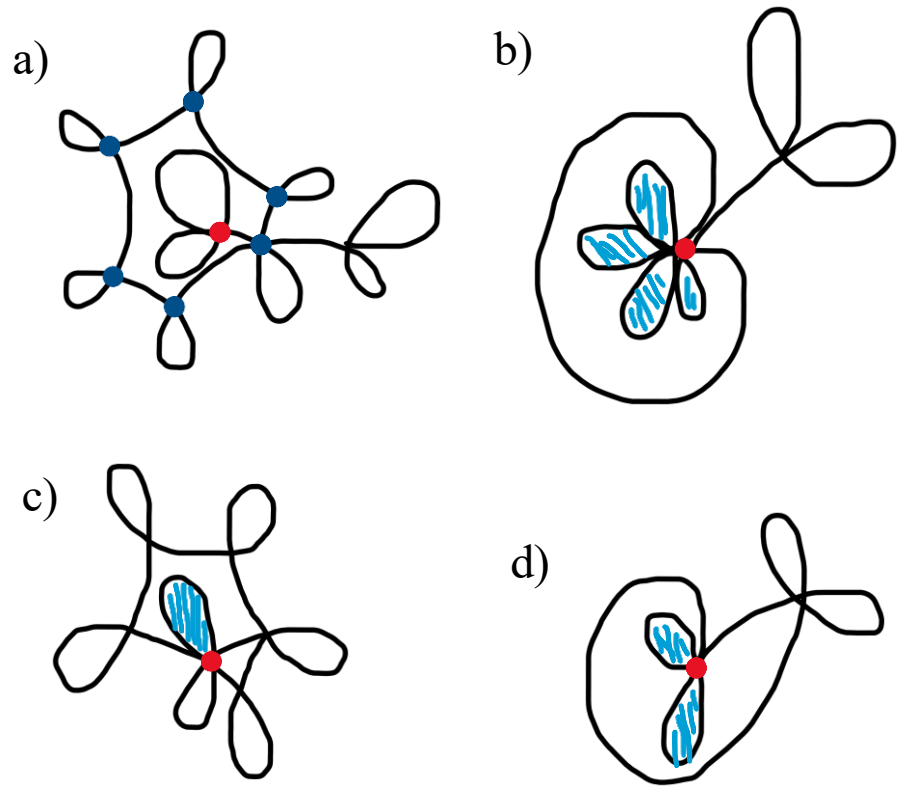
I am in my room. My room is in a hostel. And the hostel is in IIT. This description is hierarchically nested. This method of classifying one's position in space or identity could be very helpful because it clearly and distinctly sets the boundary. If we talk about its utility, there are hierarchical models across different branches of science; taxonomists use the hierarchical classification system to specify species identity, and so on. However, it may be that my position in space is not exclusive: I am in my

room, but I might also be somewhere else, thanks to the imagination. When we encounter cases such as this, the situation then becomes extremely fuzzy. For example, A can be in X and Y, and B can be in X and Z, but A and B might not be in any single group together. This violates the essence of hierarchical description, which is the equivalence relation. And to account for that, overlapping between the groups needs to be formulated.

The hierarchical nested structure was quite useful for taxonomists of those days and today's evolutionary biologists. On the contrary, there are places, for example, let's say, niche theory, genomics, and food web interaction, where the nestedness would not strictly follow, and so the partial overlapping between the groups (figure 2.) must be sought. Although researchers have used overlapping clustering in networks to describe some phenomena, I am not making a case for this here. What I am talking about, on the contrary, is the cyclical depiction of floral diagrams, which give rise to different types of coverings (figure 3.)



**Figure 2. (Top) Hierarchical nested and (Bottom) Partial Overlapping Classification System** (Baum & Smith, 2013). The top row presents a nested classification of eight species, where each species is marked by a dot, and the taxa are outlined with ovals. The bottom row illustrates an overlapping classification, with taxa depicted using ovals or arch-like shapes.



**Figure 3. Types of coverings in floral diagrams.** a) **Complete covering:** a node (red) with its leaves is completely covered in a six-node loop. b) **Self-covering:** leaves (shaded in blue) of a node are nested in its own leaf. c) **Partial overlapping:** only one leaf (shaded in blue) out of the two of a node is nested in a five-node loop. d) **Complete overlapping:** all leaves of a node are nested in a two-node loop.

## 1.2. Various Routes

I must clarify at this junction that due to the underlying metaphysical character of these diagrams, whatever reasoning or arguments I shall develop, nevertheless, will follow, by the act of generalization, in every domain of scientific study. In other words, the route I am taking—an evolutionary ecology route, as you shall see later—is just one thicket out of many branches, which must be explored and examined as a starting point. And if I had been a trained physicist, surely, I would have taken a quantum mechanical route, so to speak, because, as these diagrams are the production diagrams, the events, which are the unit of natural occurrence, must also produce at the quantum levels according to the depiction of floral diagrams.

Our thoughts are liquid. The readjustment of our reasoning and arguments from one route to another defines the character of the entities ingressed into that route. Hence, the ideas developed for the evolutionary ecology may only work for that particular route, and completely different sets of explanations are demanded to expound, let us say, a quantum mechanical route, which, as I said before, I am not able as of now.

Additionally, recently, a new route became possible to think about: the genotypic-phenotypic route, where the nodes—unlike in the evolutionary ecology route, the nodes being an environmental type—here are genes. The petals are the area of the potential phenotypic expression level of the genes.

In Chapter 2, I will begin with a concrete problem of ecosystem resilience so that we have at least something to chew on from the very outset. Later in the chapter, I shall illustrate how this problem is coupled with the problem of scale and patterns in ecology. The next chapter discusses the potential solutions and approaches and how the floral diagrams could help us shed light on how the community maintains its equilibria. In Chapter 4, is a digression into the genotypic-phenotypic route. In the final chapter, future directions are discussed.

## Chapter 2

### What is “balance” in Communities?

Ecologists have long debated whether natural communities tend toward a stable equilibrium or instead remain in constant flux. G. Hutchinson expressed that, far from the equilibrium, most of the communities are constantly changing due to the seasonal changes and intermediate growth rates of species (Hutchinson, 1953). Only a few communities that contain rapidly reproducing species or slowly reproducing species attain a stable equilibrium. He argued, therefore, that in natural conditions, the “happy balance” is almost never afoot.

While his arguments are sound and reasonable, he presented the case from the Volterra-Gause principle that “an equilibrium may actually be occupying niches which are largely distinct.” This principle, although correct in its own right, is misleading for the analysis here to begin with. To see the equilibrium of an ecosystem or a community from the lens of species niche-specificity and the degree of niche overlaps, it must be misplaced and an over-simplification of the potential equilibrium of an ecosystem, which, for several ecologists, is inherently dynamic and resilient. Recently, Blake and his colleagues have experimentally shown that evolution can shift the resilience of an ecosystem to avoid tipping into an alternative stable state (Blake et al., 2024).

Therefore, a proper criterion for measuring the “balance” of the natural communities is essential. First of all, due to the practical benefits of “balance,” our equations become “easy.” Next, the steady state is the complex function of species richness, direct and indirect species interactions, resistance (the ability of a community to remain unperturbed), and resilience (“the capacity of an ecosystem to absorb the disturbances while maintaining its function and avoiding tipping into an alternative stable state”) (Chaparro-Pedraza, 2024), and evolutionary dynamics. To make things even more complicated, these patterns are, in turn, dependent on the scales from which we measure. The relationship between patterns and scale is the most fundamental because it underpins how we perceive,

analyze, and understand the organization, dynamics, and evolution of living systems across levels –from molecular interactions within cells to species distribution across biogeographical realms – revealing the processes that generate biodiversity and sustain ecosystem functioning. Seeing the importance of this relationship between scale and pattern, much emphasis has been put on disentangling it (Levin, 1992).

However, the floral diagrams are universal and the structures, although differently, will apply invariantly across different scales.



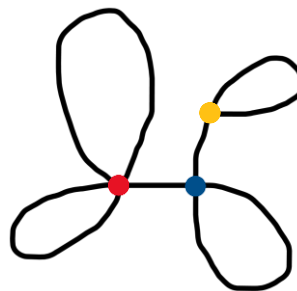
## Chapter 3

### The Evolutionary Ecology Route

The conditions that apply to make an equilibrium community, as discussed in the previous chapter, are muddled partly because of the scale pattern obscurity. Can the floral diagrams shed light on what conditions stabilize the community?

In the evolutionary ecology route, the floral diagrams could be seen as the patterns of equilibrium community, where each node is an environmental type and leaves of the node – the space within which inter-trophic species coexist.

Following this, the question immediately strikes as to why the same environmental type would have multiple leaves and what it means for the no. of nodes to form a loop with each other. And anyway, what is this environmental type to begin with? To answer these questions, totally new ideas have been developed that do not share the rich history of ecological literature. In the next section, I shall discuss these new ideas, give the criteria of equilibrium, and integrate these ideas to explain the enigmatic features of the floral diagrams on the face of this EE route. Since these ideas are not grounded in the current ecology literature, later in the last section of this chapter, a few criteria of the equilibrium are discussed from the current ecology theories that come closest for practical purposes.



**Figure 4. Different environmental types.** PE<sub>1</sub> system (red node), PE<sub>2</sub> system (dark blue node), and PE<sub>3</sub> system (yellow node)

### 3.1. $P = cE$

Life is a song that is sung by each and every organism but in different modes. Just like the equalizer has discrete frequencies and volume to adjust different modes, organisms have the same discrete properties in different volumes and order. However, each species of organism has unique volumes and order of these discrete properties, giving them different modes of behavior and function.

The big assumption I am making is that there is an original arrangement of these discrete properties (P) that the community of different species tends towards. In other words, there is some orchestric constant (c) that drives the modalities of organisms. The interlocking of the community of organisms shall only occur when the internal differences of properties of organisms living in space-time meet that constant. Of course, the environmental term (E) also must be there (Hutchinson, 1953). The event of intersection denotes the environmental type that characteristically bends the constant term. The equation then becomes as follows:

$$P = cE \quad (1)$$

### 3.2. Mirroring effect

If we consider the effects of continuity on the organismic domain, all organisms are internally related to one another because they are, after all, in the continuous field. To imagine this, we need to dive back into the period of the origin of life. The production of variations always confounded many thinkers of evolutionary sciences, including Darwin himself. Here, I am assuming there were some variations in the events that potentially ended up as a part of life processes. But more things could be said before we can say they were that part a) the variations in their character were due to the continuous field, and b) their existence implies that they were internally related to each other.

Consider what Leibniz stated in his Monadology: "...each individual monad reflects the entire universe, but does so through its own

unique perspective, creating a personalized mirror of the world based on its own nature and level of perception....”

To reiterate the idea of internal relations in Leibniz’s language, I will say that each organism mirrors the properties of other organisms in space through its own unique properties that make up its mode of living. Hence, the modalities of events, or shall I say, in this context, organisms, are seamlessly mirrored, meaning they are involved in the activities due to their past as well as the future.

Mechanistic metaphysics reigned in our procedure of collecting data and thinking so well that we have perhaps forgotten to consider the indirect pathways of transmitting information from one organism of one group of species to another group of species. Ecologists may talk about energy flows and ecosystem coupling (Sánchez-Hernández, 2025), but how dominant are these causes in their view? I think we have just begun to appreciate indirect agents in governing the stability of ecosystems (Sánchez-Hernández, 2025). The mirroring effect puts the problem of causality to an end by assuming reasoning that all organisms are internally related due to the continuous field. This is the most important reason why the networks of an ecological food web, which has the tendency to account only for direct interactions, may not be adequate.

### **3.3. Reflective Time and Evolvability**

One event of intersection would mean that the community of organisms in space has mirrored each other through their own unique properties that make up their modes of living. Note that such interlocking of the community of organisms would only take place when the equation provided before is met. The time taken to do so is the reflective time of the PE system. Imagine, literally, an organism moving its mirror, constantly changing the angles and readjusting it until the whole community in which it lives stabilizes. Similar readjustments are done by all the organisms in space until everyone mirrors each other. The time taken to reach this state is the reflective time of the entire PE system. The final orientation of

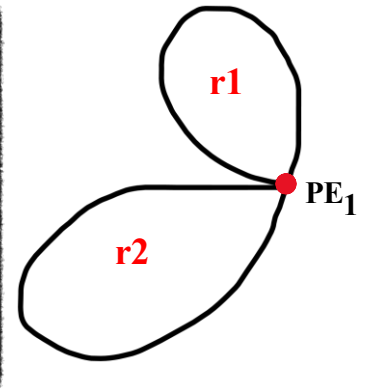
mirrors of the organisms that give rise to the interlocked community is the evolvability of the entire PE system.

In the endurance of this PE system, the community evolves together, meaning each local adaptation is reflected in the other in a certain way.

The one with the sharp eyes will notice immediately that here, the evolution is not some local change in the traits of the population or interacting species (coevolution), but it is the global change within the community that occurs at their characteristic reflective time.

Furthermore, if we consider a family of PE systems, the reflective time would be distinct, and also, therefore, their way of evolving (evolvability). This distinct quality also determines the propensity of spatial boundary (rule 6 of the floral diagram) (figure 5.).

**Figure 5. A family of PE<sub>1</sub> systems:** the reflective time of r2 is more than of r1 as much as their propensity of space. This virtually means that for any local changes in order for it to be mirrored at a global level (in all the organisms living in space), r1 will take less time than r2. The consequences presumably are that the evolutionary trajectories of organisms in r1 and r2 will be remarkably different.



### 3.4. Properties of Organisms are the criteria of equilibrium

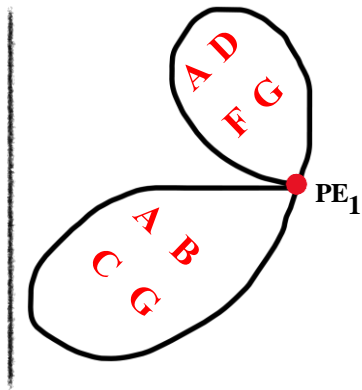
The difference in the value of reflective time in both the leaves (figure 5.) also means that properties of their community composition, though more or less quantitatively similar, may have been arranged in a different order and in different degrees or have different types of organisms altogether.

$$P(r1) \sim P(r2) \quad (2)$$

Corollary to this, the global evolution of species in both the communities of r1 and r2 has different trajectories at their characteristic

reflective time while preserving the value of  $P$ . However, it does not follow from this that the modalities of species will be necessarily completely different. As depicted in figure 6, species A is common in both  $r1$  and  $r2$ . An immediate question would strike: what kind of changes will we observe in species A ( $r1$ ) and species A ( $r2$ ), and to what extent? This I cannot tell; it totally depends on the way global evolution occurs in  $r1$  and  $r2$ .

**Figure 6. Species in  $r1$  and  $r2$  of a family of the  $PE_1$  systems.** Though the group of species in  $r1$  and  $r2$  are different (A, D, F, G in  $r1$  and A, B, C, G in  $r2$ ), the quantitative value of  $P(r1)$  and  $P(r2)$  will be approximately the same.



What I can predict, interestingly, is that the evolutionary trajectories of A, B, and C in  $r2$  and A, D, and F in  $r1$  are coupled, respectively. Since the floral diagram is a conceptual figure, and that, in reality, species are found altogether in a community, totally mixed, I predict that if, through a certain empirical measure, we found, let's say, species A has two evolutionary trajectories (it could be genetic or phenotypic diversity), and we also found species G to have two evolutionary trajectories, then it will follow that the species A and G with same evolutionary trajectory are tightly coupled. This will be clear in the next section, where I will use elemental stoichiometry to make this prediction.

### 3.5. What do the properties of organisms constitute?

Till now, I have been evading the meaning of what these properties actually are in the organism. I did mention through the music metaphor that they are modes of organisms, but that is not properly scientific and helpful. So, in the current literature on ecology, is there anything that comes anywhere near to the descriptions of the properties that I am eluding here?

As we need observables that have quantitative insights, the search possibly reduces to two different approaches in ecology, prominent in their

own respect—namely, trait-based ecology (Klausmeier et al., 2020) and ecological stoichiometry (Stephens et al., 2015).

Trait-based ecology is founded on linking the functional and heritable aspects of organisms to the entire community structure. It has become quite useful in predicting climate-induced changes in community patterns, enabling conservation managers to study the effects of invasion and disentangle the underlying mechanisms and dynamics of changes in community structure.

Alternatively, the framework of ecological stoichiometry has come a long way. It is about measuring the elemental ratios (C:N:P) to understand how organisms interact in a community with the resources and other occupants available. It is an extremely powerful approach, in my view, because just by virtue of elemental ratios, we can describe several eco-evolutionary phenomena. Recently, this has been united with the evolutionary dynamics of intraspecific variations (here, elemental and classical variations within species) to understand ecosystem patterns and processes (El-Sabaawi et al., 2023).

Now, I want to demonstrate how ecological stoichiometry might be the closest to the conception of properties I described in terms of its utility by explaining the prediction in its language.

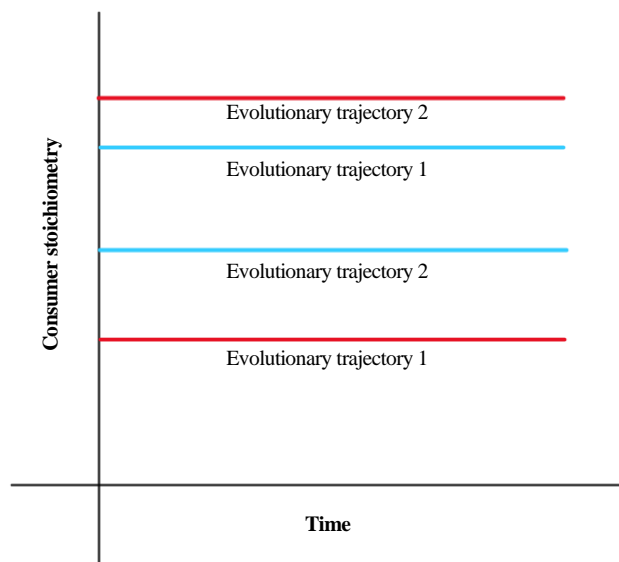
Consider some elemental ratios, such as the ratio of phosphorous and nitrogen (P:N). If we find the consumer stoichiometry (P:N) of species A remains constant through time but has variation within species (see figure 9.), it means that species A has two evolutionary trajectories. Suppose the community follows the floral structure (two leaves of a node) (figure 6.). If we also found the same trend in the consumer stoichiometry of species G with two evolutionary trajectories, then the set of species A and G with the same evolutionary trajectory must be tightly coupled. In other words, the variant of A is affected by the variant of G.

Not only this but the moment we get an idea of the floral structure of the communities, we can predict, based on perturbation experiments, which species are coupled with which sets of species (figure 7.). However, it is to be seen in the case of complex floral diagrams how the behaviour of evolutionary coupling comes out to be. For instance, (figure 7.) illustrates a

constant bifurcation curve with respect to the consumer stoichiometry and time. It can most likely be not as simple as that. Perhaps with time, the consumer stoichiometry may change. Perhaps the leaves in which these species live themselves overlapped, partially or completely (figure 3.), in a loop of PE systems, rendering our experimental methods dubious and impotent. These are dangerous perhapses.

However, on the bright side, the whole question of equilibrium communities transforms into the question of evolutionary coupling and floral (ecological) structure. This looks like progress.

It is known that if the rate of adaptation of species in the ecosystem is slower than the rate at which perturbation occurs, the ecosystem disintegrates. In other words, perturbations with a frequency higher than the reflective time of the PE system would lead to its collapse. Knowing which sets of species in the space are responsible for lower reflective time will be a key to understanding the equilibrium communities. And here, floral diagrams shall chip in to provide us a proper blueprint. I admit we are quite remote from seeing this possibility materialize at this moment.



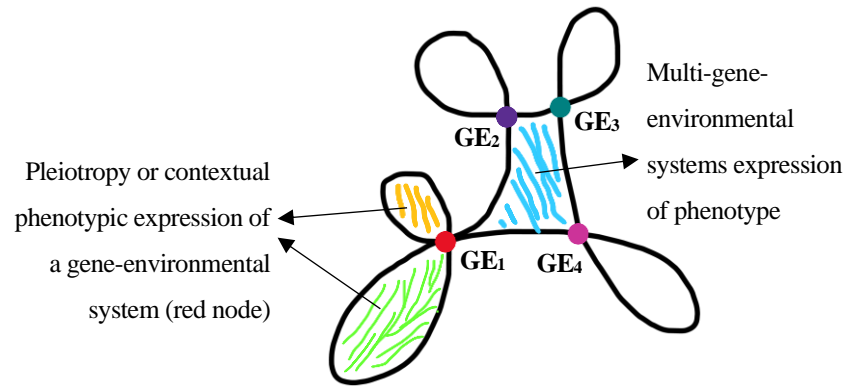
**Figure 7. Consumer Stoichiometry vs Time.** Blue line represents sets of species A bifurcating into two evolutionary trajectories 1 and 2, and the red line represents sets of species G bifurcating into two evolutionary trajectories 1 and 2. A set of species A and G with the same evolutionary trajectory are evolutionarily coupled. This means that the

community is most likely following the floral structure of the  $PE_1$  system: two leaves on a node. This also means that lower-scale dominant animals (bacterial communities, for example) at a comparable scale of species A and G must have both or any one evolutionary trajectory, following the same floral structure as species A and G. In other words, even though the bacterial community in space shared with species A and G has several genetic diversities, at the scale of species A and G, the genetic and phenotypic diversity that defines the consumer stoichiometry of the bacterial community in that space must be divided into two sets.



## Chapter 4

### The Genotypic-Phenotypic Route



**Figure 8. Multi gene-environmental (MGE) systems-loop.** The  $GE_1$  system has a family of leaves (yellow-shaded and green-shaded) and is involved in the MGE system's expression of the phenotype (blue-shaded). Its leaves represent either pleiotropy (effects on multi-traits) or contextual phenotypic expression.

As depicted (figure 8.), the node in this route becomes the gene-environmental system, and the leaf becomes its phenotypic expression. The node is not only a gene but also the representation of the genotype-environmental interaction via the expression of different phenotypes in different contexts (leaves). In other words, the existence of more than one leaf on the same node is a function of the environment of the gene. But, the changes in the expression of phenotypes in different contexts may not be major: either it affects the fitness value, or it has a different effect depending on the context, but with, more or less, the same functional aspect.

Another case, that is of pleiotropy (one gene affecting multiple traits) must not be undermined. It is a specialized case of contextual expression of phenotype, where the functional aspect is so disconnected that the context itself crystallizes into a particularly distinct trait.

The yellow-shaded and the green-shaded leaves can either represent pleiotropy or contextual phenotypic expression. This raises an ambiguity as to what is which. Where we stand in our analysis, it seems far-fetched to distinguish between both cases. Worse, the genotypic-phenotypic route remains totally conceptual, and we do not know how to

map the experimental data of genes and their expression levels onto this representation. All that we have currently is the knowledge of different types of coverings (figure 3.) and of this possible route to examine various biological scenarios.

## **Chapter 5**

### **Future Directions**

Evolution and ecology are littered with confounding terminologies and problems, such as pattern changes due to scale effects. To emerge out of this conceptual Gordian knot with the simplest, adequate, and consistent explanation is the ultimate task of a scientist. The types of coverings—I have not mentioned the other type here, but one can make out—reduce the possible biological scenarios to five major categories of coverings, and it is now up to us whether we are deeply interested in unraveling the meaning and rules behind different permutations of these coverings in different biological contexts.

This I cannot see being done without creating a new mathematics for floral diagrams—mathematics that describes the relation of a node or a leaf or a loop with all the nodes and leaves and loops in a way that it changes with the addition or removal of nodes and leaves and loops. Such base relations will certainly tell abstractly the meaning of the categories of coverings. Furthermore, once applied to any of the two routes, they will help us elucidate the evolutionary coupling relations or the genotypic-environmental-phenotypic relations.

# REFERENCES

## JOURNAL ARTICLE

- Archibald, E. E. A. (1949). The Specific Character of Plant Communities: II. A Quantitative Approach. *The Journal of Ecology*, 37(2), 274. <https://doi.org/10.2307/2256609>
- Arrhenius, O. (1921). Species and Area. *The Journal of Ecology*, 9(1), 95. <https://doi.org/10.2307/2255763>
- Baum, D. A. ., & Smith, S. D. . (2013). *Tree thinking: an introduction to phylogenetic biology*. W.H. Freeman and Company.
- Blake, C., Barber, J. N., Connallon, T., & McDonald, M. J. (2024). Evolutionary shift of a tipping point can precipitate, or forestall, collapse in a microbial community. *Nature Ecology & Evolution*, 8(12), 2325–2335. <https://doi.org/10.1038/s41559-024-02543-0>
- Chaparro-Pedraza, P. C. (2024). Evolution alters ecological resilience. *Nature Ecology & Evolution*, 8(12), 2155–2156. <https://doi.org/10.1038/s41559-024-02542-1>
- Chen, B., Jiang, J., & Zhao, X. (2019). Species-Area Relationship and Its Scale-Dependent Effects in Natural Forests of North Eastern China. *Forests*, 10(5), 422. <https://doi.org/10.3390/f10050422>
- El-Sabaawi, R. W., Lemmen, K. D., Jeyasingh, P. D., & Decleck, S. A. J. (2023). SEED: A framework for integrating ecological stoichiometry and eco-evolutionary dynamics. *Ecology Letters*, 26(S1), S109–S126. <https://doi.org/10.1111/ele.14285>
- Gleason, H. A. (1922). On the Relation Between Species and Area. *Ecology*, 3(2), 158–162. <https://doi.org/10.2307/1929150>
- Hanson, C. A., Fuhrman, J. A., Horner-Devine, M. C., & Martiny, J. B. H. (2012). Beyond biogeographic patterns: Processes shaping the microbial landscape. In *Nature Reviews Microbiology* (Vol. 10, Issue 7, pp. 497–506). <https://doi.org/10.1038/nrmicro2795>
- Hutchinson, G. E. (1953). *The Concept of Pattern in Ecology* (Vol. 105).
- Klausmeier, C. A., Kremer, C. T., & Koffel, T. (2020). Trait-based ecological and eco-evolutionary theory. In *Theoretical Ecology*

- (pp. 161–194). Oxford University Press.  
<https://doi.org/10.1093/oso/9780198824282.003.0011>
- Ladau, J., & Elie-Fadrosh, E. A. (2019). Spatial, Temporal, and Phylogenetic Scales of Microbial Ecology. In *Trends in Microbiology* (Vol. 27, Issue 8, pp. 662–669). Elsevier Ltd.  
<https://doi.org/10.1016/j.tim.2019.03.003>
  - Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73(6), 1943–1967. <https://doi.org/10.2307/1941447>
  - Sánchez-Hernández, J. (2025). Climate-induced shifts in ontogenetic niches threaten ecosystem coupling. *Trends in Ecology & Evolution*, 40(3), 224–227.  
<https://doi.org/10.1016/j.tree.2024.11.018>
  - Stephens, J. . P., Berven, K. A., Tiegs, S. D., & Raffel, T. R. (2015). Ecological stoichiometry quantitatively predicts responses of tadpoles to a food quality gradient. *Ecology*, 96(8), 2070–2076.  
<https://doi.org/10.1890/14-2439.1>
  - Whittaker, R. J., Willis, K. J., & Field, R. (2001). Scale and species richness: Towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, 28(4), 453–470.  
<https://doi.org/10.1046/j.1365-2699.2001.00563.x>
  - Yanai, I., & Lercher, M. (2019). Night science. In *Genome Biology* (Vol. 20, Issue 1). BioMed Central Ltd.  
<https://doi.org/10.1186/s13059-019-1800-6>