

Ecosystem Concepts: Complexity/Chaos/Scaling, part 1

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We know ecosystems experience lots of diversity, due to evolution and the many species that co-exist. The object of this lesson is to seek order in the chaos. What rules emerge to describe ecosystems, their function and structure? How big can you be? How many individuals can you sustain? What are the rates of exchange you can sustain? How do you study a complex ecosystem with so many different actors? Answers to these questions start to arise through examination of scaling, complexity and chaos.

Topics

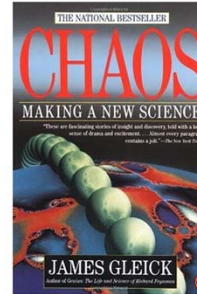
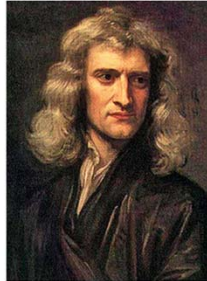
- Ecological Systems and Complexity
- Hierarchy of Processes and the Time and Space Scales on which they Operate
- Self-Organization and Emergent-Scale Properties

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We are Experiencing a Paradigm Shift from a Clock-like Mechanical, Newtonian View of how the World Works to one based on an acceptance and understanding of Complexity

Studying an Ecosystem as a Complex systems forces us to think and act differently in how we study, quantify, predict, manage and manipulate complex systems



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We have to think differently when studying ecosystems and the biosphere around us. This takes us from a conventional Newtonian approach, where the world seems clocklike, to one that embraces chaos and complexity. Lessons derived here also can play roles in understanding advances in economics, climate, political science and health. We all are complex systems. Treating these systems in this manner help us understand better how to manage these systems and understand the limits of our ability to predict future states.

EcoSystems are Complex Systems

What Does this all Mean?



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Attributes of Complex Adaptive Systems is described Next

Attributes of Complex Adaptive Systems

- Many Coupled Processes
 - With Non-Linear Response to Forcing
 - Subject to Positive and Negative Feedbacks

$$y = a + bx + cx^2$$

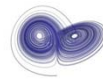
- Hierarchical System
 - Microbe to Biome

$$y = a \cdot x^n$$

- Multiple-scales
 - Power Law Behavior

$$\frac{dc}{dt} = kc$$

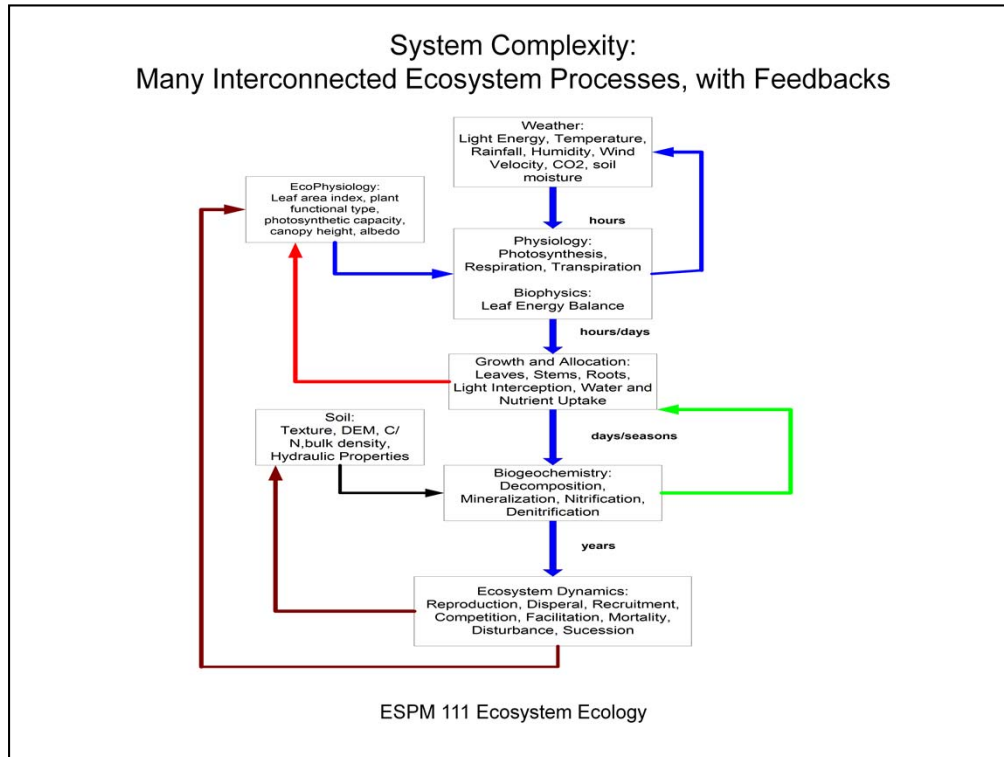
- Deterministic/Predictable
- Sensitive to Initial Conditions
 - Path dependency
- Self-Organization
- Scale-Emergent Properties
- Resiliency and Robustness



Sum of parts does
not = whole

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This is the list of many attributes of complex systems. I will explore these more in the following slides



Good example of the coupled processes and some feedbacks that are experienced in an ecosystem..There is a hierarchy of space and time scales as we move through this flow chart. Space scales can emerge from microbe and organelle to the biome. Time scales can operate at fractions of seconds, for photosynthesis and assimilation, to centuries and millenia for ecosystem dynamics and soil formation

Landscapes Form Non-Linear Systems



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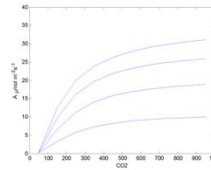
Geomorphology is a good example of the formation of complex river patterns and non linear forcing through interactions with the landscapes. We will see in later lectures the presence or absence of vegetation can have a marked role on the shape rivers and streams take as they carve out the landscape.

Non-Linear Biophysical Processes are Ubiquitous in Ecology

Photosynthesis

$$A \sim \frac{aI}{b+cI}; \frac{dC}{e+fC}$$

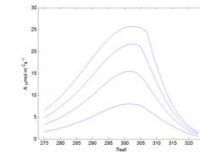
$$aA^3 + bA^2 + cA + d = 0$$



Transpiration

$$e_s(T) \sim \exp(T)$$

$$aLE^2 + bLE + c = 0$$

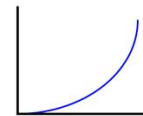


Respiration

$$R_d \sim \exp(T)$$

Leaf Temperature

$$L\uparrow \sim T_s^4$$

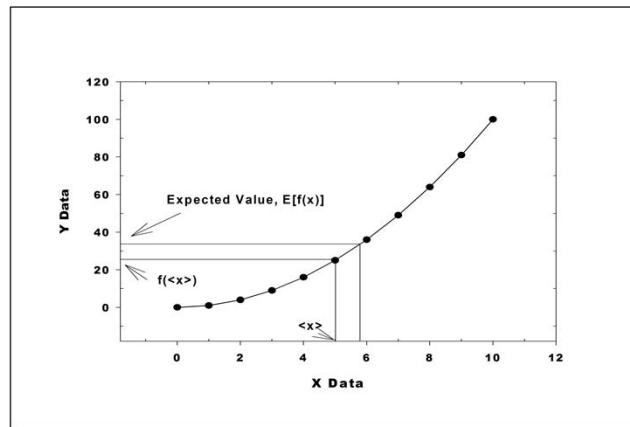


Here is an example of some of the major non linear functions that are used to quantify ecological processes. Do know the shape of the response curves that emanate from these curves.

Why do We Worry about Non-Linear Processes?

The Mean of the Non-Linear Function Does Not Equal
the Function of the Mean

$$\overline{f(x)} \neq f(\bar{x})$$



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Why do I, a humble biometeorologist, worry about non linearity. It is because we need to assess non linear functions that are dependent upon the environmental state of the leaves. Yet the function of the mean DOES NOT equal the mean of the function. Ideally we are more concerned with evaluating the mean of the function.

Hierarchy

- Hierarchy is defined as the arrangement of some entity (space, time, organism) into a graded series of compartments
- Hierarchies are nested in that each level is made up of a group of lower levels

EP Odum (1996)

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The idea of complexity and hierarchy may be in fashion, after the publication of James Gleick's book *Chaos*, but it is no so new in ecology. Eugene Odum was on to idea in in his books, Barry Osmond and Paul Jarvis were early proponents of hierarchy, and when I was a young scientist at Oak Ridge, Bob O'Neill was promoting Hierarchy theory in the 1980s

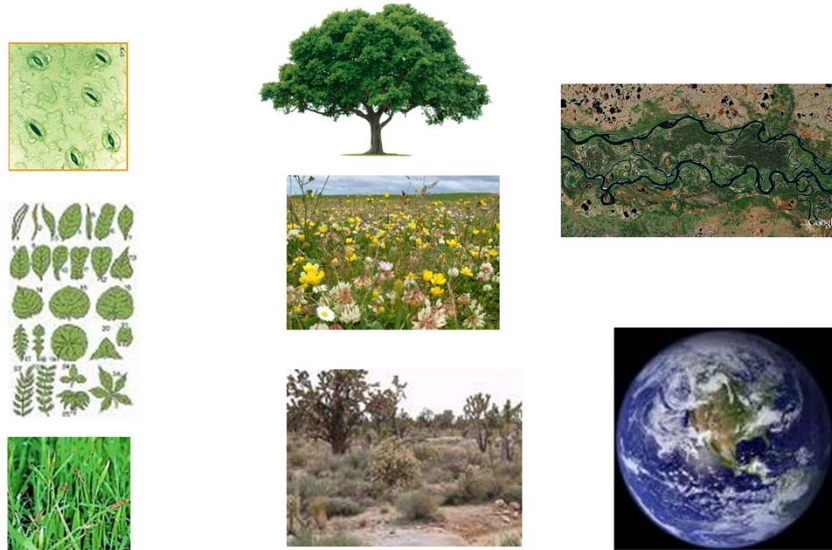
Biological/Ecological Hierarchy

- Organelles
- Cells
- Organ
- Organism
- Population
- Ecosystem
- Landscape
- Biogeographic Region, Biome
- Biosphere

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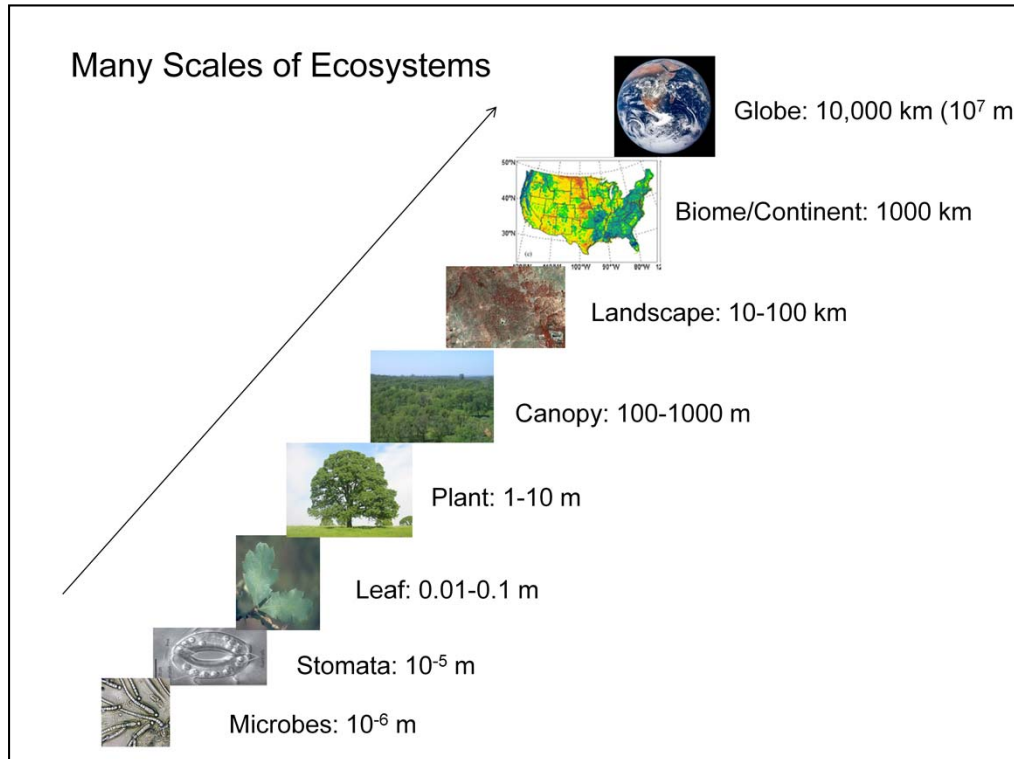
When we think about hierarchy, it is clear that the lower level scale cannot function alone without its connect to the higher order system. Organelles are just a pool of protoplasm without the confines of a cell. Cells will die, without the supply of resources from organs, organs depend on the circulation of the organism. Organisms will go extinct without its connection to a population. Populations depend upon resources of an ecosystem and the state of the ecosystem depends upon the climate and soils of the landscape, region and biome

Hierarchy of Ecologically-Relevant Space Scales



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Stomata, Leaf, plants, communities, landscapes, regions/continents/globe



Ecology is complex in many ways, one is the fact that we must distill and assess information and processes that span over 15 Orders of Magnitude. Compare this with Rocket science, essentially the ballistics of a missile. This is more complex than 'rocket science'

Ecosystems Operate across a Hierarchy of Time and Space Scales



Fast
and
Small



Large and Slow



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Visual idea of hierarchy of time

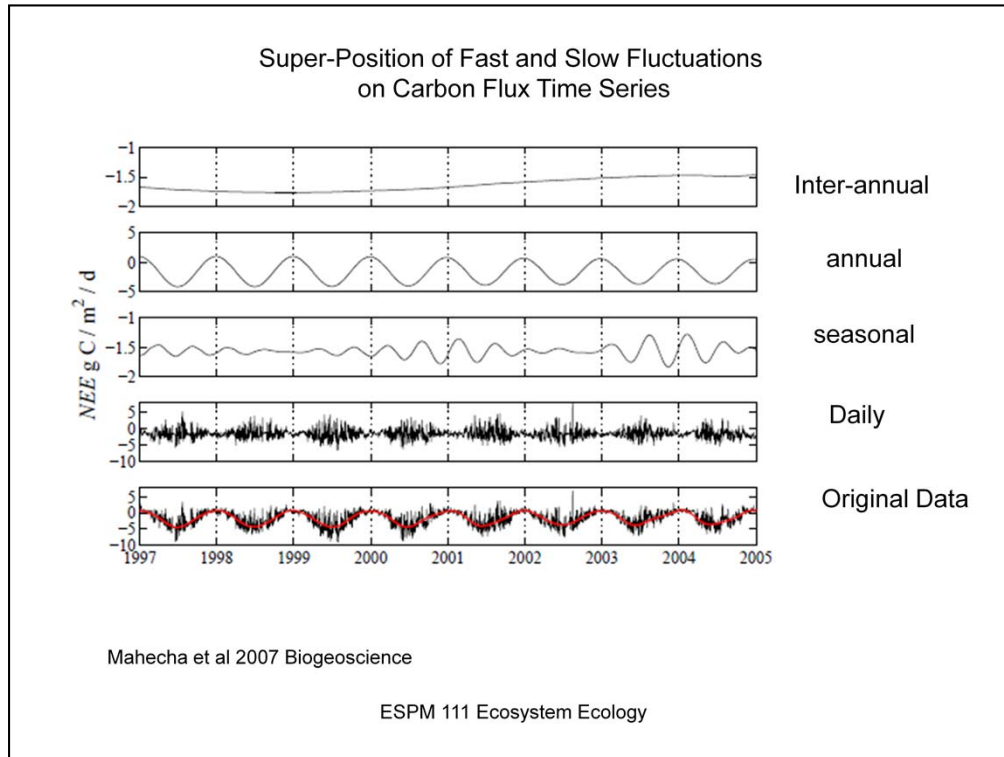
Critical Time Scales



- **Hourly/Daily**
 - Physiology
 - Photosynthesis, Respiration, Transpiration, Stomatal Conductance
- **Seasonal & Annual**
 - Net and Gross Primary Productivity
 - Autotrophic and Heterotrophic Respiration and Decomposition
 - Plant Acclimation
 - Mineralization and Immobilization
- **Decadal**
 - Competition, Gap-Replacement, Stand Dynamics
 - Changes in Soil Organic Matter
- **Century**
 - Succession, Mortality
- **Millennia**
 - Species migration
 - Soil Formation
- **Geological Periods**
 - Evolution, Speciation, Extinction
- **Eons**
 - Evolution of Life

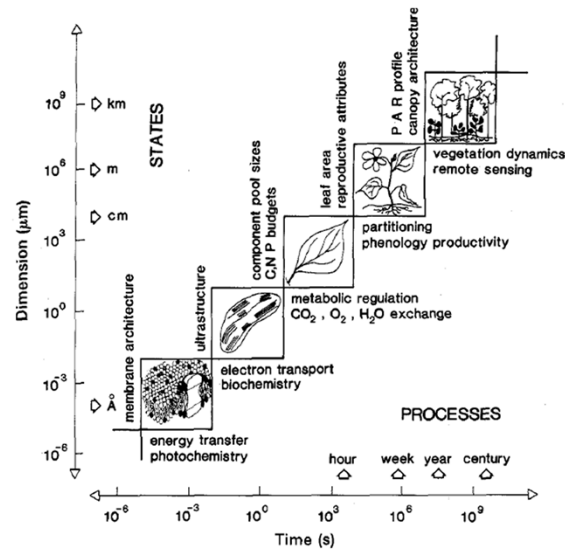
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Key time scales to understand and why



Examples of the super-positioning of fast and slow processes on the exchange of CO₂ flux measured over many years.

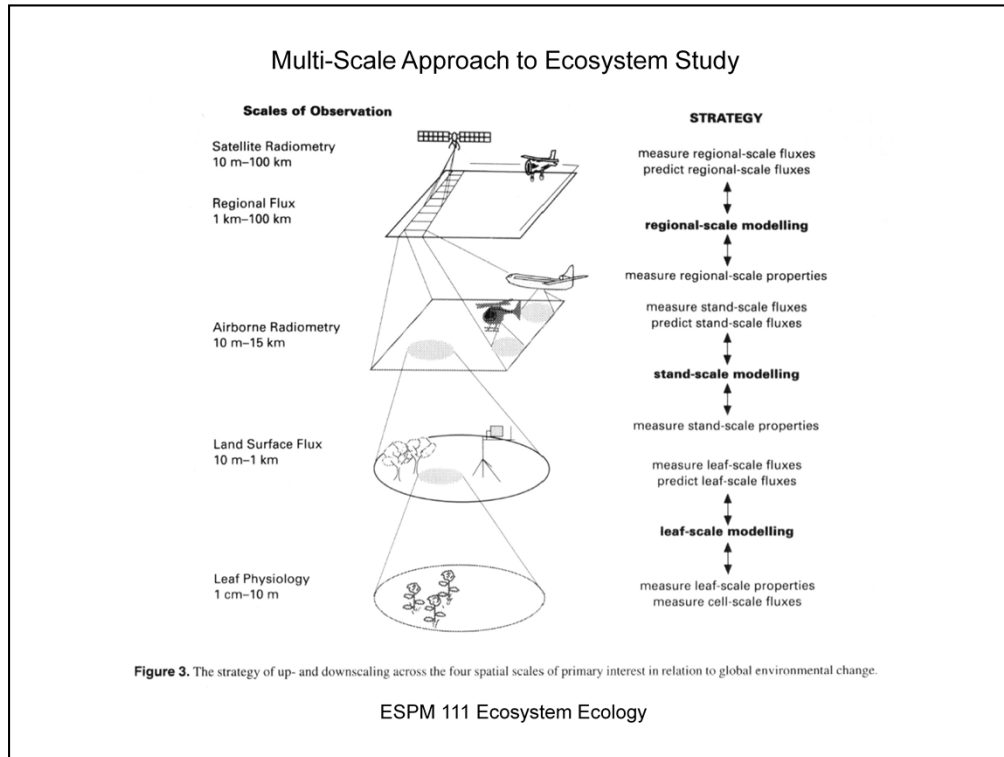
Hierarchy of Ecological Processes and States of Life, Spans 14 orders of Time and Space



Osmond and Chow, 1988 Aust J Plant Physiol

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Summary of the time and space scales of import.



The multi-scale problem reveals the reality that there is no one way or sensor to study the entire biosphere or ecosystem. We have to adopt a hierarchal approach. This forces us to blend physiological studies at the leaf and soil plot scales with micrometeorological flux towers, networks of towers and finally satellite, or aircraft, remote sensing to upscale and add everything up. Then all this information can be ingested into, or distilled by, models

Scale Emergent Properties

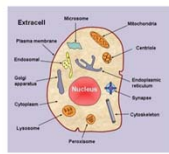
..' a cell is more than its molecules, as an organ is more than its cells, and as an organism is more than its organs, in a food web, new structure emerges at every organizational level up to and including the whole web'

Cohen et al 2009, PNAS

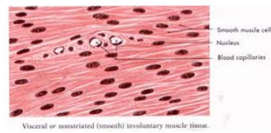
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One of the reasons I am fascinated with complexity is the idea of scale emergent properties. The whole acts differently than the sum of the parts

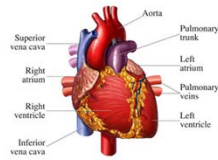
Example of Scale Emergent Property, v1



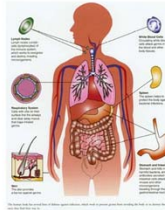
Cells



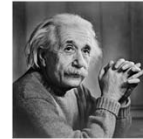
Tissue



Organs



Body



Thought, Language, Creativity



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The idea, 'scale emergent property' may sound odd or foreign. But it is all around us. Humans are good examples of the idea of scale emergent properties

Example of Scale Emergent Property, v2

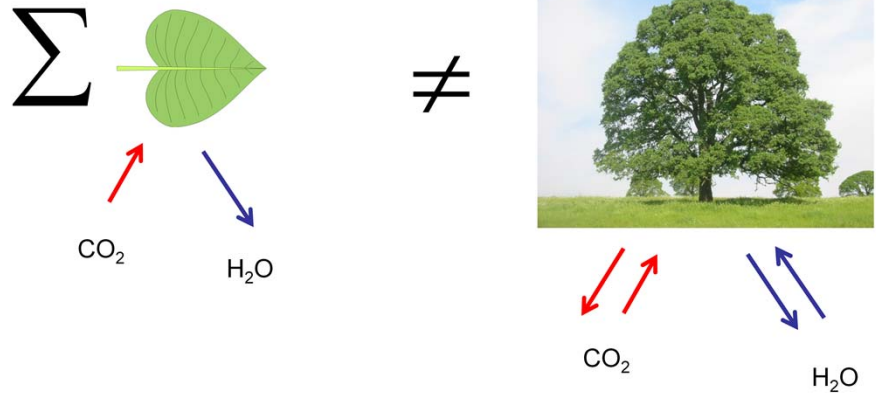
Melting Ice Cube vs Melting Glacier



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The melting of ice is complex and is something that needs to be factored better into global climate change models if we are to correctly predict the melting of the ice caps with warming, and understand their albedo feedbacks

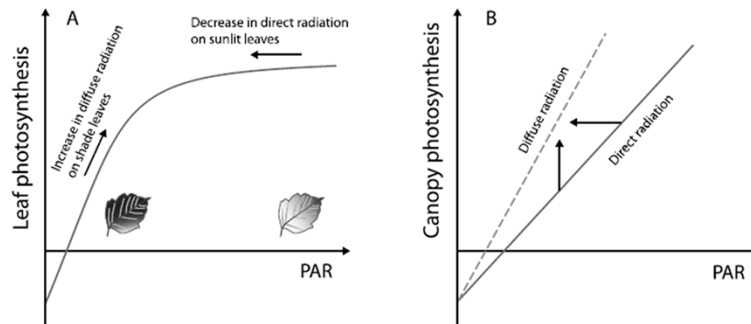
Scale-Emergent Properties of Ecosystems



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In my realm, the sum of leaves acts differently than how the whole ecosystem functions, with regards to CO₂ and water vapor exchange

Example: The Behavior of How Photosynthesis of a Leaf and Canopy Respond to Light

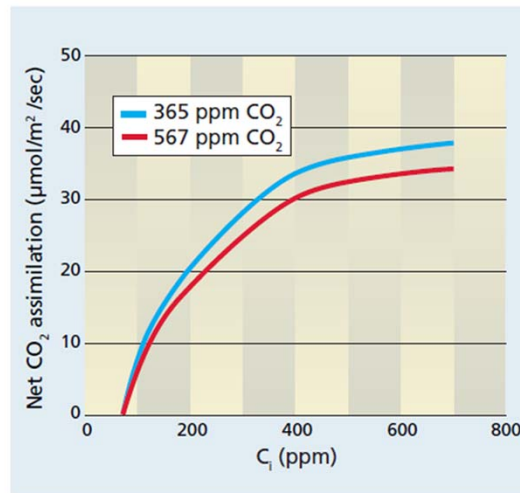


Knohl and Baldocchi 2008 JGR-Biogeosci

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The light response of photosynthesis of a leaf differs from that of a canopy. The leaf photosynthesis saturates with increasing light levels. Canopy photosynthesis has a linear response and its slope depends on the fraction of diffuse light!; e.g. the quality and directionality of the light

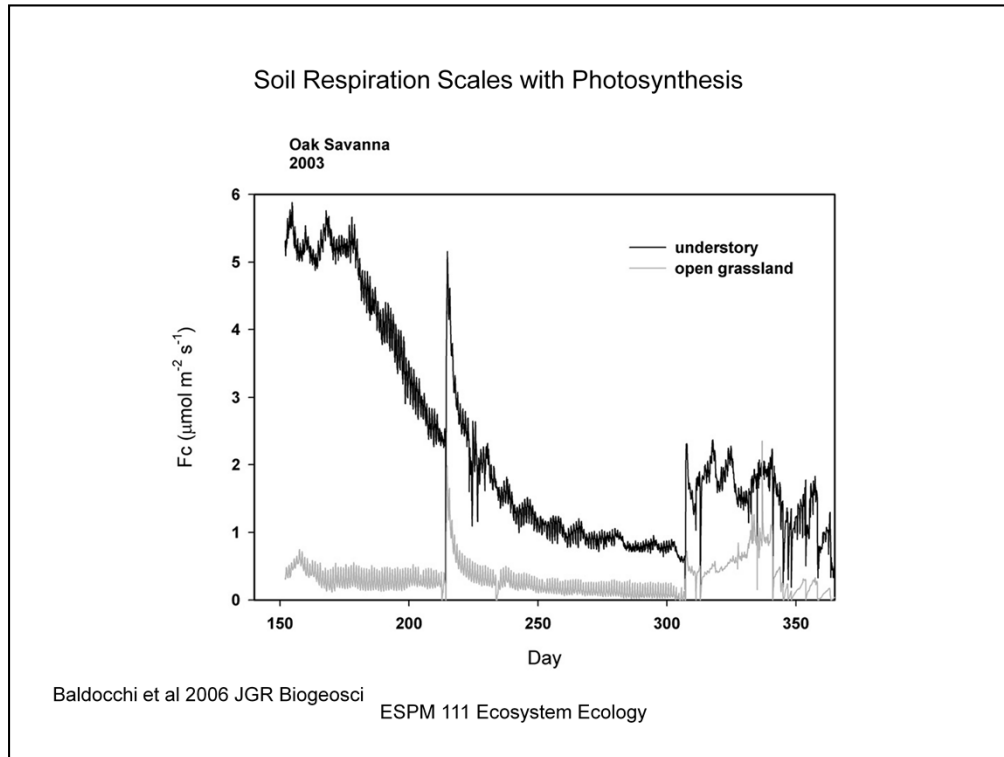
The Response of Photosynthesis to CO₂ depends upon its CO₂ and Nitrogen Growth Environment



Ainsworth and Rogers 2007, PCE; adapted from Bloom, 2009 Cal Ag

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Down regulation of photosynthesis to CO₂ and its growth environment is another example of a scale emergent property



Soil respiration differs greatly where there are plants photosynthesizing and at what rates the plants are photosynthesizing. Exudates from roots of recent photosynthesis drives microbial respiration. I am very pessimistic we can ever partition soil autotrophic respiration from heterotrophic respiration from this fact, without introducing artifacts. Please prove me wrong and come up with a great idea. It will revolutionize the field.

Scale-Emergent Properties

- Whole $\neq$ Sum of Parts
 - Photosynthesis and Light
 - Leaf Photosynthesis is non-linear and saturating function of light and is independent of diffuse light
 - Canopy Photosynthesis is a quasi-linear function of light and a strong function of diffuse/direct light
 - Photosynthesis and CO₂
 - Leaf Photosynthesis increases non-linearly with CO₂
 - Canopy photosynthesis experiences a down-regulation due to feedbacks with decomposition of plant matter and release of nutrients and decreases in stomatal conductance
 - Evaporation
 - Leaf is a function of humidity deficits and net radiation
 - Canopy is a function of net radiation minus Soil Heat flux
 - Tree roots tap ground-water
 - Tree transpiration is scale invariant at the landscape scale.
 - Albedo
 - Optical Properties of many green leaves are similar
 - Forests are darker than grasslands and absorb more energy
 - At regional scale, forests evaporate water vapor, which forms clouds and increases the planetary albedo
 - Ecosystem Respiration and Rain
 - Rain promotes heterotrophic respiration of decomposing litter, but does not promote elevated plant metabolism
 - Rain-Induced induced Respiration Pulses are Greater in the sun (due to photodegradation) than in the shade ESPM 111 Ecosystem Ecology

Over the years I have been trying to compile a list of scale emergent properties in ecology. Here is my partial list. Missing anything?

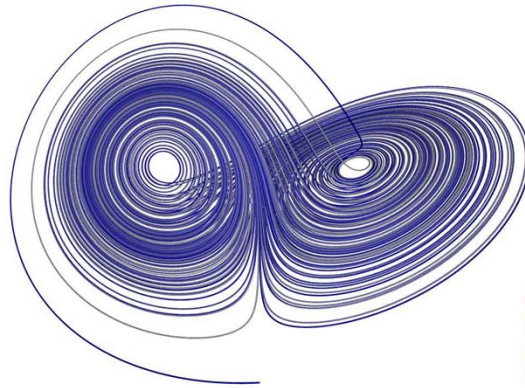
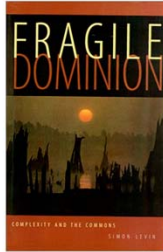
- Complexity is not the same as Random, it is **Deterministic**
- Simple sets of Coupled Ecological or Meteorological Differential Equations ($dx/dt=f(x)$) can produce Complex Behavior
 - Lord Robert May, Nature, 1974
 - Ed Lorenz, J. Atmos Sci, 1963



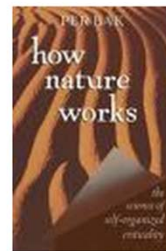
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Complexity ideas evolved from simple toy models used to predict wind and predator prey relations. Even with perfect equations, under certain conditions chaos emerged!

**Complexity:
Creating Order out of Chaos and Establishing the Limits on Predictability**



Lorenz Attractor



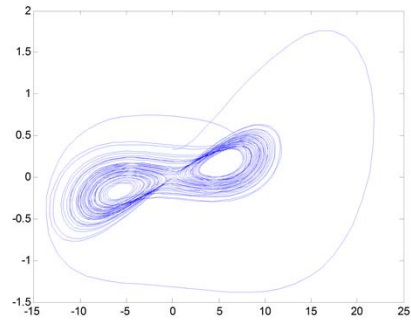
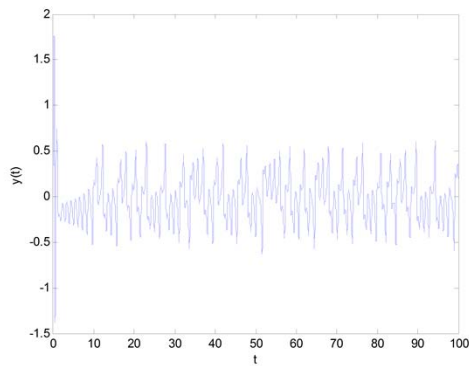
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Butterfly Effect: If a butterfly flaps its wings can a Hurricane form? Idea is that complex systems are sensitive to initial conditions

Solving Lorenz Equations with Simple Matlab Code

solves the set of equations

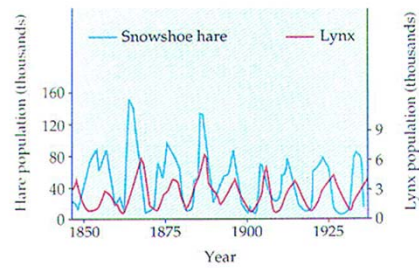
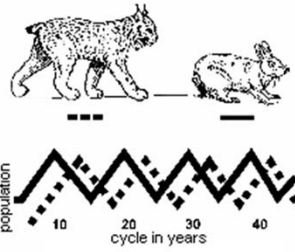
```
%  
%    $x' = b y - c (x - x_{\text{star}})$   
%    $y' = x z - y$   
%    $z' = -x y - (z - 1)$ 
```



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Simple matlab code can be used to play with the Lorenz equations.

Chaos and Complexity in Predator-Prey Dynamics



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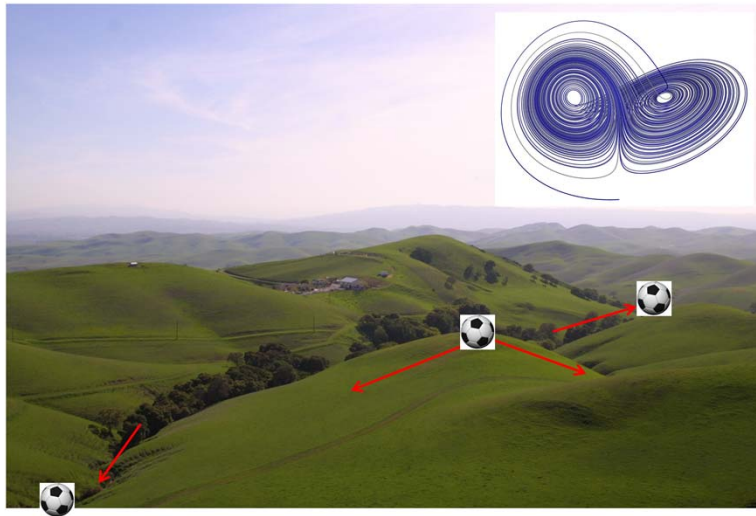
Example of Self-Organization
Polygons in the Tundra



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One beauty of chaos theory is that there can be self organization. In this picture we see polygons form in the tundra. Hurricanes and tornadoes are other examples

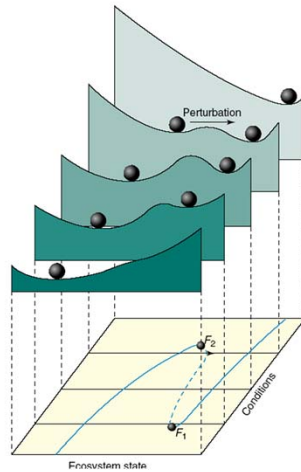
Sensitivity to Initial Conditions and Path Dependence



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Lorenz found that chaos emerged due to sensitivity to initial conditions.

Non-Linearity and Complex Systems are Robust to Perturbations,
they but are subject to Regime Shifts, too



A Lesson and Warning
for Unintended
Consequences, when
Perturbing Complex
Systems

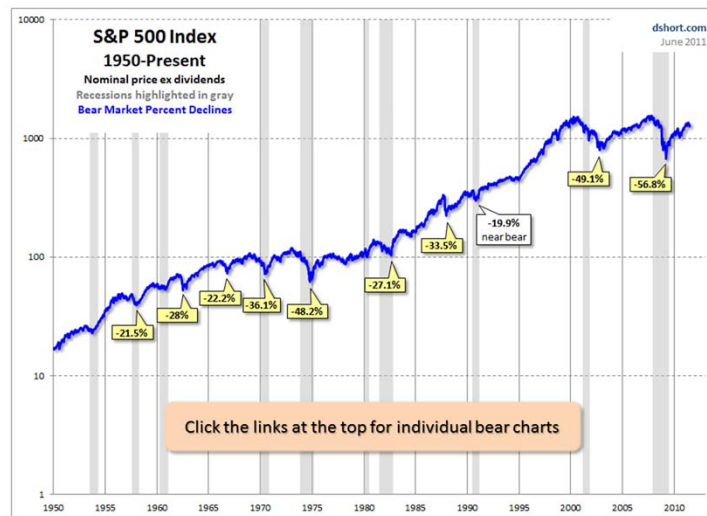
An Example of the Delicate balance between
Stability and Collapse

Scheffer and Carpenter, 2003 TREE

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The many feedbacks of complex systems produce robust systems, until there is a regime shift. It is my opinion that this robustness is causing society to be cavalier about global warming. The climate system has been fairly robust to our initial insults by changing greenhouse gas forcing. But ultimately, glaciers will melt, permafrost will release vast stores of methane and CO₂, and we will enter a new climate state.

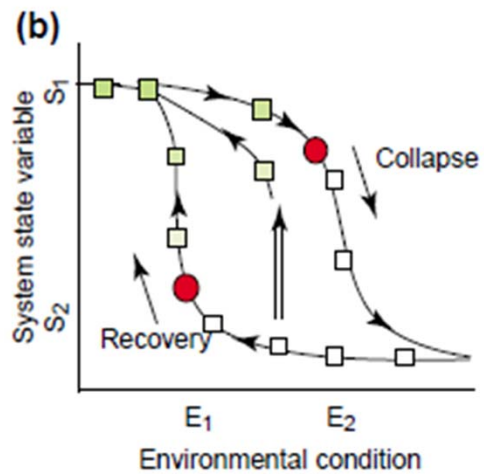
Example: Periodic Crashes in the Stock Market,
Another Complex System



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Stock Market also experiences crashes. Problem with chaos theory is that from it we know crashes will happen. We just can't predict when with any accuracy. So expect crashes. Plan and be cautious of bubbles.

Hysteresis—another non-linear response--in Ecology



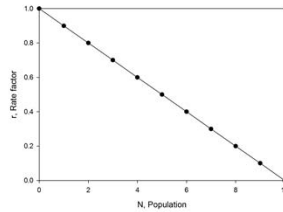
Suding et al 2004 TREE

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Hysteresis, another word of the day, is behavior of complex systems. The transition of an ecosystem from state 1 to state 2 does not follow the same path as it recovers from state 2 back to state 1. Kate Suding, a fellow faculty member, has written a lot on this topic.

Chaos from a Deterministic Equation,
The Change in Population, N , is a function of a growth rate, r ,
that is a linear function of the Population, N

$$\frac{dN}{dt} \approx \frac{\Delta N}{\Delta t} = N \cdot r(N) = N r \left(1 - \frac{N}{K}\right)$$



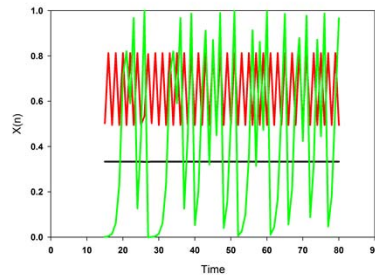
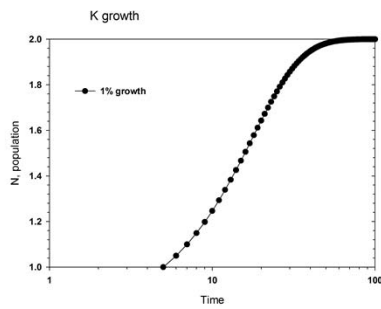
Example of Negative Feedback: Population increases, causes the rate
of Population increase to Decrease

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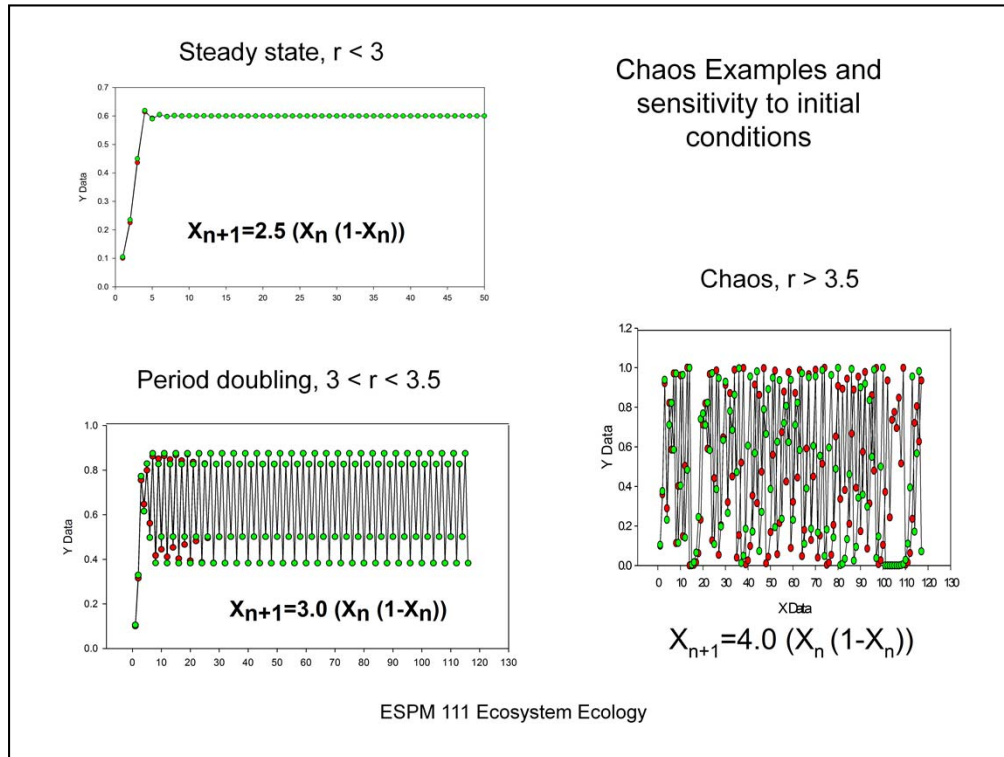
Simple equations to play with on excel to see chaos behavior. Simple logistic growth equation. Change r and see what happens

$$\frac{dN}{dt} \approx \frac{\Delta N}{\Delta t} = N \cdot r(N) = N r \left(1 - \frac{N}{K}\right)$$

Logistic Eq. Population Growth:
 $N_{t+1} = N_t(1+r(1-N_t/K))$

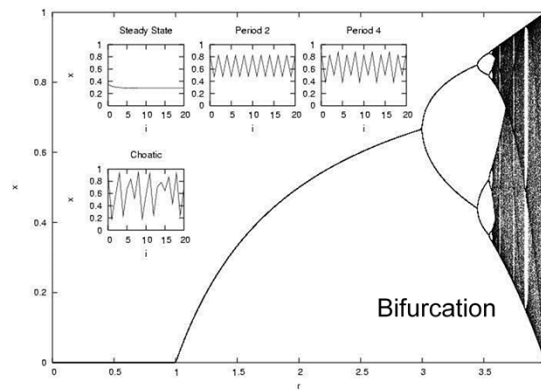


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I confess the high r values, >3 , for inducing chaos, tend not to happen for many populations, which grow more on the order of 1 to 10% (0.01 to 0.1). Though it may be possible for microbes.

Chaos from a Recursive Equation $x_{n+1} = r x_n(1-x_n)$



Steady-State, $r < 2$
 2 pt cycle: $2.526 > r > 2$
 4 pt cycle: $2.656 > r > 2.526$
 8 pt cycle: $2.685 > r > 2.656$
 Chaos: $r > 2.692$

May, 1974, Nature

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Summary

- Ecosystems are Complex Adaptive systems
- Ecosystems work across a hierarchy of time and space scales that span over 14 Orders of Magnitude
- Ecosystems are Resilient to small Perturbations
- Ecosystems are Vulnerable to Switching States, if Pushed too Hard, and may Experience Hysteretic Response on Recovery
- Managing Complex Systems Forces us to Think and Act Differently

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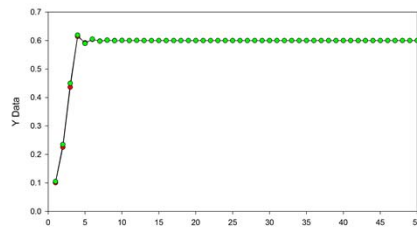
Discussion Material

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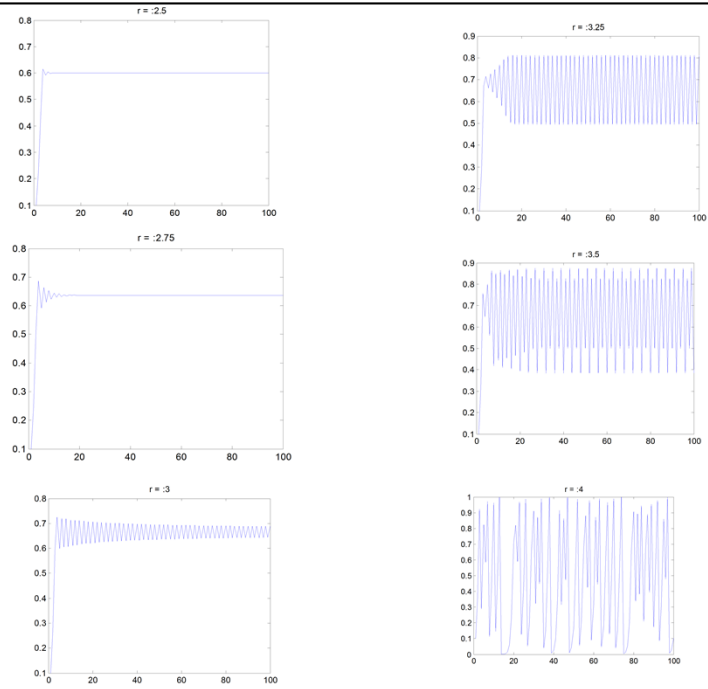
Apply this Simple, Iterative Equation to an Excel Spreadsheet, or R/MATLAB code & modify the Coefficient (1, 1.5, 2, 2.5, 3, 3.5, 4) and plot

Change initial conditions slightly and see if they converge to common values, or not

$$X_{n+1} = 2.5 (X_n (1 - X_n))$$



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Critique to Everyday Applications

Ideal Growth for Individual Species, no Competition or Interactions

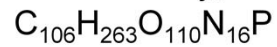
Most Plants and Ecosystems grow at a rate of a few percent ($r = 0.01, 0.05, 0.1$),

Not at rates of 250+%, so they may not experience chaos

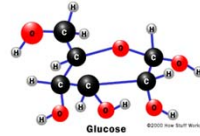
Conversely this theory is applicable for rapid growing populations, like bacteria, insect pests, so growth rates of 200 to 300% are plausible

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Ecological Stoichiometry, CO₂-H₂O-N-P



- CO₂
 - Primary source of high-energy sugars, CH₂O
- Nitrogen
 - Key component in RUBISCO, the enzyme that fixes CO₂, and amino acids that form proteins
- Phosphorus
 - Key component of ATP and NADPH, the energy compounds central to many metabolic processes
- H₂O
 - Keeps cells turgid
 - Solvent for transferring nutrients through solution
 - Lost via stomata



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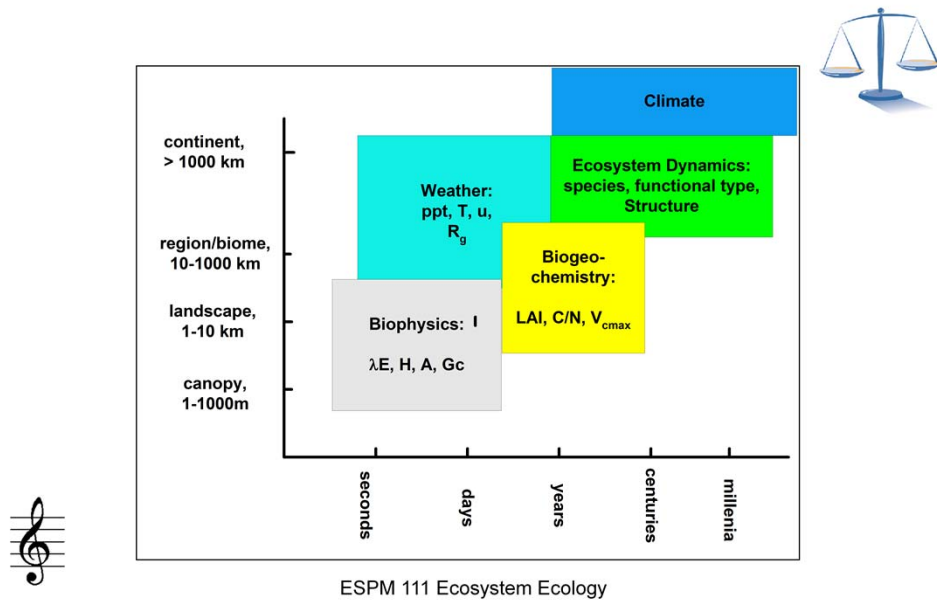
Microbes make the BioGeoChemical Cycles Revolve

'bacteria are astonishingly good at finding energy that will let them make a living. More or less everywhere the earth brings together substances with different redox potentials, there's a bacterium that knows how to take advantage of the situation by passing electrons from one to the other and skimming off energy as it does'.

Oliver Morton, 2008 Eating the Sun: How Plants Power the Planet

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Process and Rates are a Matter of Scale, too



Ecosystem as a Complex Adaptive System

- Self-Organized Criticality
 - Strange attractor in a dynamic system
 - Delicate balance between stability and collapse
 - Power-Law Behavior
- Individuality of components
 - *'Individual agents drive evolutionary change from the bottom up, so that system evolution emerges from the interplay of processes at diverse scales'*
- Localized interaction among components
 - Competition, predation and sexual reproduction exert Positive and Negative Feedbacks
- Diversity of components
 - Mutation refreshes diversity
- Autonomous Processes
- Components
 - Aggregation and Fractal Patterns
 - Non-linearity
 - Hierarchical Structure
 - Scale Emergent Processes
 - Heterogeneity of components
 - Flows of material and Energy

Levin, 2005, Bioscience; Levin, 2000, Ecosystems; Levin, Fragile Domain

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Ecosystem Ecology, the Baldocchi-Biometeorology Perspective

- **Physics wins**

- Ecosystems function by capturing solar energy
 - Only so much Solar Energy can be capture per unit are of ground
- Plants convert solar **energy** into high energy carbon compounds for **work**
 - growth and maintenance respiration
- Plants **transfer** nutrients and water down concentration/potential energy gradients between air, soil and plant pools to sustain their structure and function
- Ecosystems must maintain a **Mass Balance**
 - Plants can't Use More Water or Carbon than has been acquired
- Ecosystems are Complex Systems

- **Biology is how it's done**

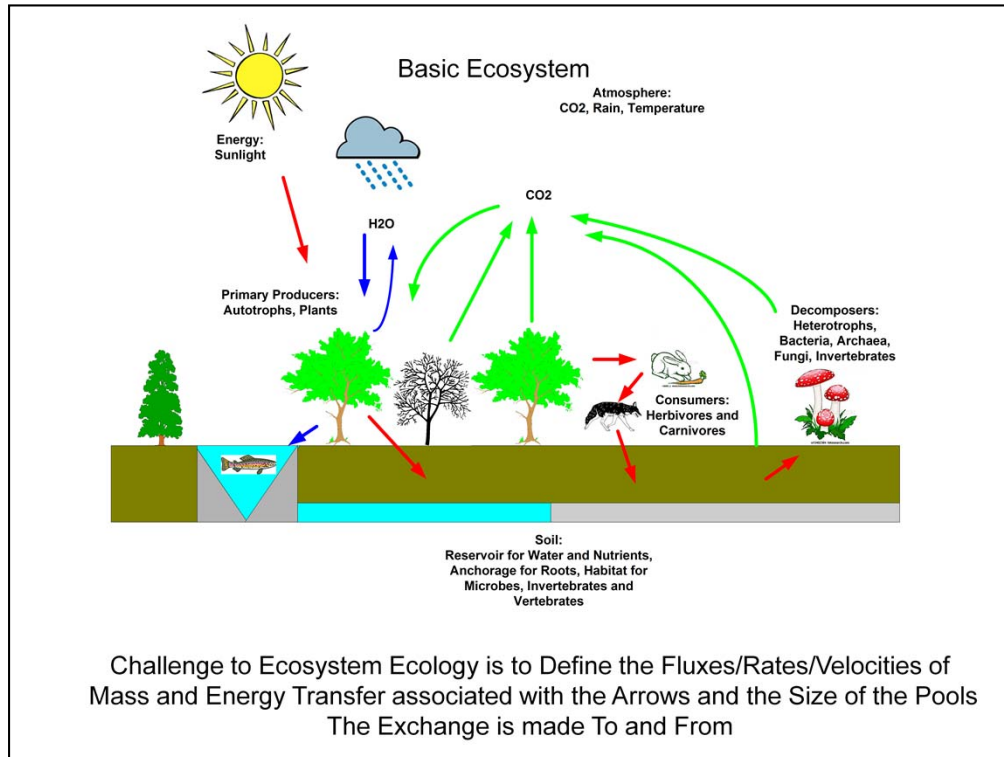
- Species differentiation (via evolution and competition) produces the structure and function of plants, invertebrates and vertebrates
- In turn, structure and function provides the mechanisms for competing for and capturing light energy and transferring matter
 - Gases diffuse in and out of active ports on leaves, stomata
- Bacteria, fungi and other micro-organisms re-cycle material by exploiting differences in redox potential; they are adept at passing electrons and extracting energy
- Reproductive success passes genes for traits through the gene pool.

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New paper

- Chave, J. (2013), The problem of pattern and scale in ecology: what have we learned in 20 years?, *Ecol. Lett.*

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Who is Present and the Flows of Energy and Matter (water, CO₂)

Ecosystem Ecology,
the Baldocchi-Biometeorology Perspective
'Physics Wins, Biology is How it's Done'



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Physics wins

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- Bacteria, fungi and other micro-organisms re-cycle material by exploiting differences in Redox Potential; they are adept at extracting chemical energy by passing electrons; Microbes are pivotal for sustaining ecosystems
- Reproductive success passes genes for traits through the gene pool.

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Corollary to Silver's Rule: 'Microbes Rule the World'



- They do, given the Energy stored in Carbon Substrate, produced by Plants, eating Sunlight and Consuming CO₂
- 'All function, and indeed all life, within an ecosystem depends upon the utilization of an external source of energy, solar radiation',
 - RL Lindeman, 1942, Ecology
- All Biogeochemical Cycles come to a Halt without Microbes and their ability to Recycle Nutrients and Extract Chemical Energy
- Bottom-Line. Plants and Microbes Work Together as a System, An EcoSystem

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