Ecosystem Concepts: Complexity/Chaos/Scaling, part 1

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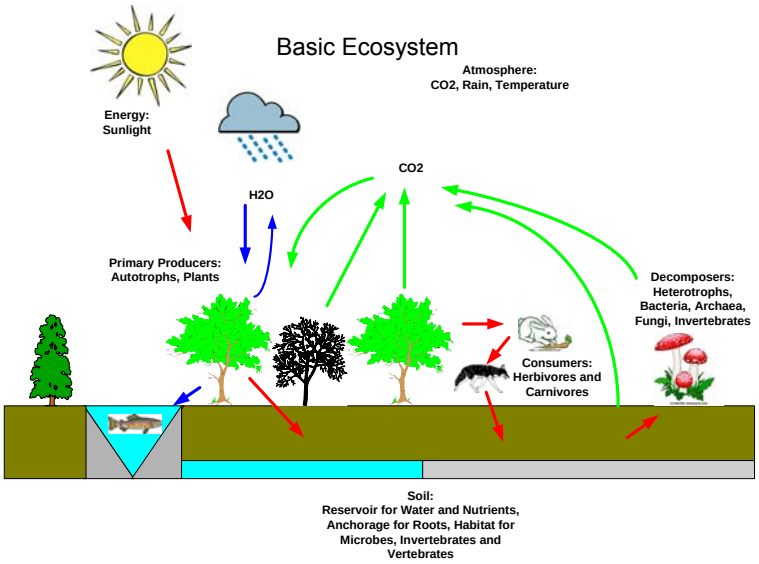
Topics

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



Challenge to Ecosystem Ecology is to Define the Fluxes/Rates/Velocities of Mass and Energy Transfer associated with the Arrows and the Size of the Pools The Exchange is made To and From

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

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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 extracting chemical energy by passing electrons; Microbes are pivotal for sustaining ecosystems
- Reproductive success passes genes for traits through the gene pool.

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 CO_2
- '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

EcoSystems are Complex, Adaptive Systems

What Does this all Mean?

Attributes of Complex Adaptive Systems

- Many Coupled Processes
  - With Non-Linear Response to Forcing
  - And Subject to Feedback
- Hierarchal System
- Multiple-scales
  - Power Law Behavior
- Deterministic/Predictable
- Sensitive to Initial Conditions
  - Path dependency
- Self-Organization
- Scale-Emergent Properties
- Resiliency and Robustness

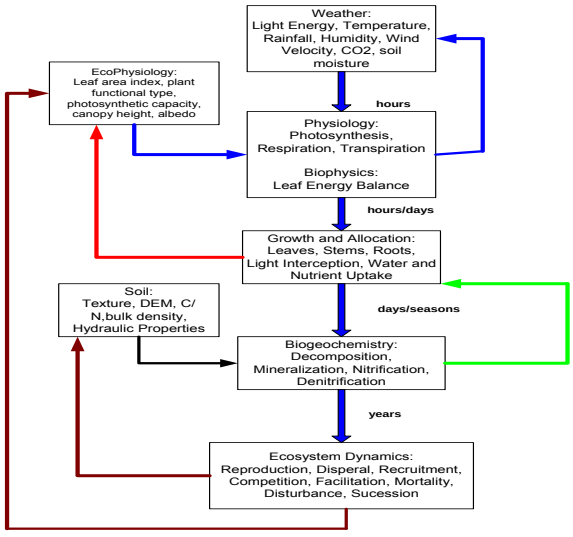
$$y = a + bx + cx^2$$

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

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

Sum of parts does not = whole

System Complexity:
Many Interconnected Ecosystem Processes, with Feedbacks



Landscapes Form Non-Linear Systems

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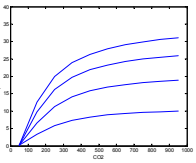
Non-Linear Biophysical Processes are Ubiquitous in Ecology

Photosynthesis

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

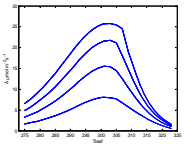
$$aA^3 + bA^2 + cA + d = 0$$



Transpiration

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

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

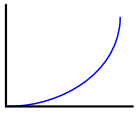


Respiration

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

Leaf Temperature

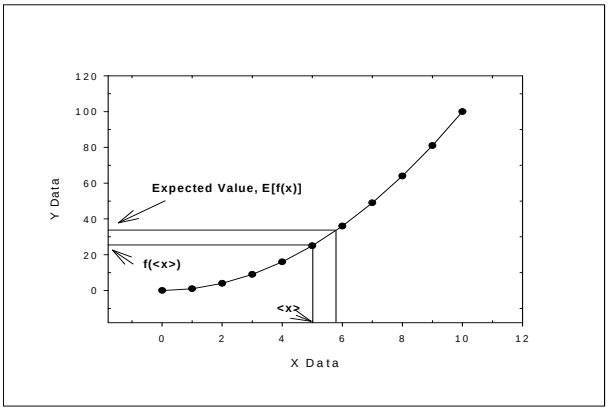
$$L\uparrow \sim T_s^4$$



Why do We Worry about Non-Linear Processes?

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

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



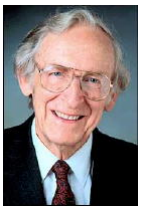
Ecosystems Operate across a Hierarchy of Time and Space Scales

Fast and Small

Large and Slow

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)

Biological/Ecological Hierarchy

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

Hierarchy of Ecologically-Relevant Space Scales

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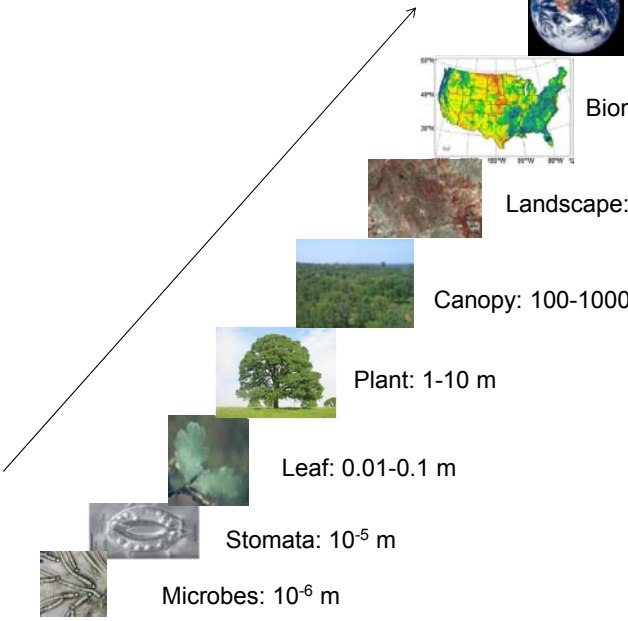
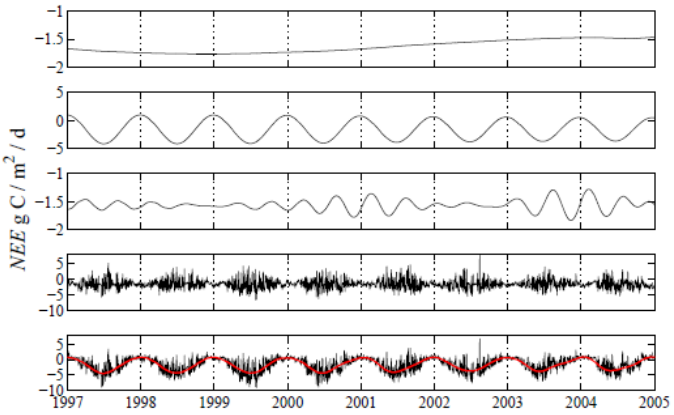
Many Scales of Ecosystems



Critical Time Scales

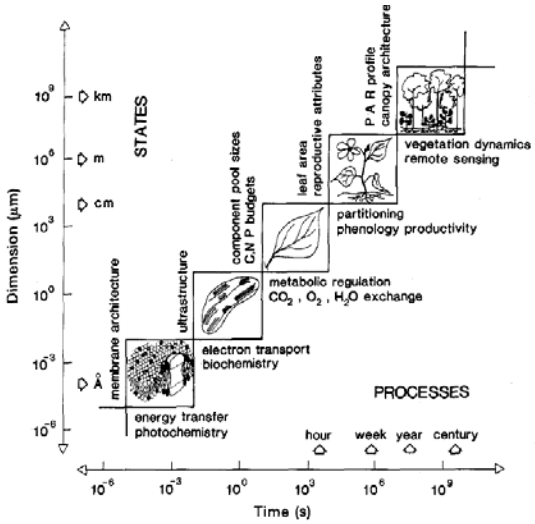
- **Hourly/Daily**
  - **Physiology**
    - **Photosynthesis, Respiration, Transpiration, Stomatal Conductance**
- **Seasonal & Annual**
  - **Net and Gross Primary Productivity**
  - **Autotrophic and Heterotrophic Respiration and Decomposition**
  - **Plant Acclimation**
  - **Mineralization and Immobilization**
- **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**

Super-Position of Fast and Slow Fluctuations on Carbon Flux Time Series



Mahecha et al 2007 Biogeoscience

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



Osmond and Chow, 1988 Aust J Plant Physiol

ESPM 111, Ecosystem Ecology

Multi-Scale Approach to Ecosystem Study

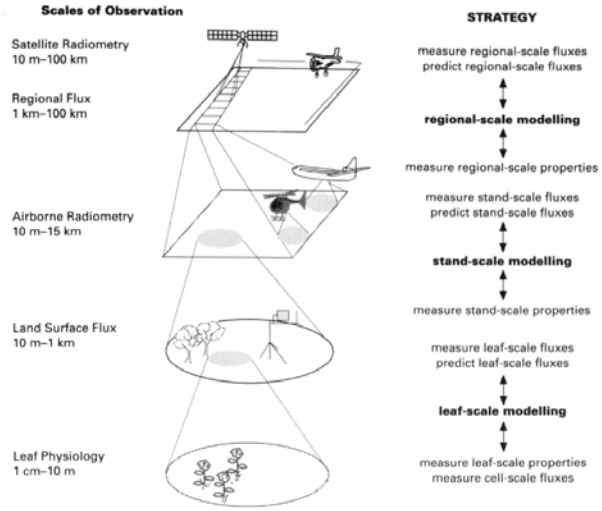


Figure 3. The strategy of up- and downscaling across the four spatial scales of primary interest in relation to global environmental change.

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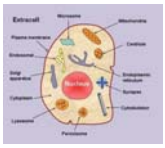
Scale Emergent Properties

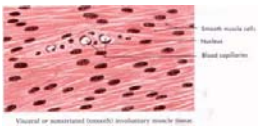
..' a cell is more than its molecules, as an organ is more than its cells, and as an organism is more than its organs, in a food web, new structure emerges at every organizational level up to and including the whole web'

Cohen et al 2009, PNAS

Example of Scale Emergent Property, v1

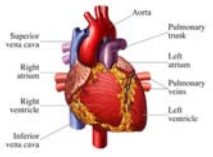


Cells

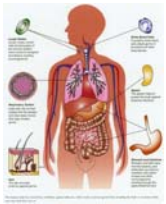


Tissue

Thought, Language, Creativity



Organs

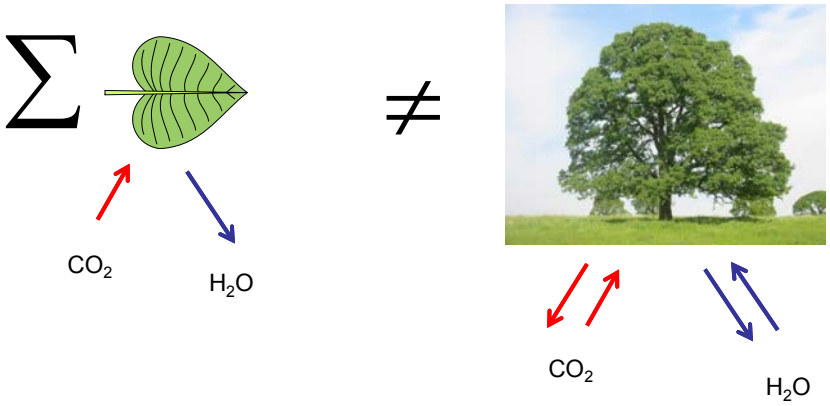


Body

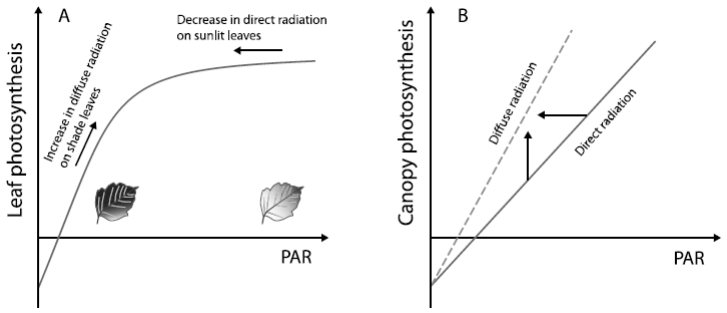
Example of Scale Emergent Property, v2

Melting Ice Cube vs Melting Glacier

Scale-Emergent Properties of Ecosystems

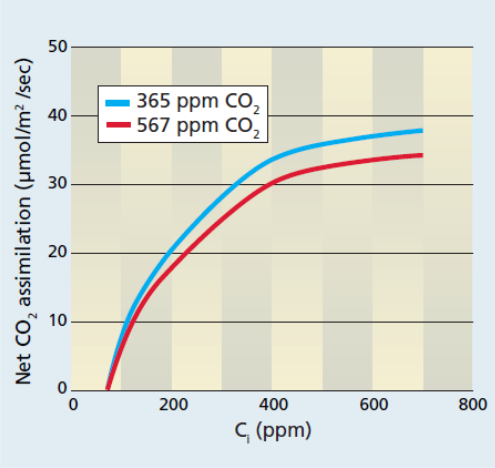


Example: The Behavior of How Photosynthesis of a Leaf and Canopy Respond to Light



Knohl and Baldocchi 2008 JGR-Biogeosci

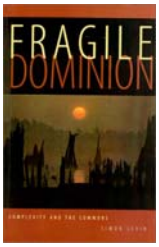
The Response of Photosynthesis to CO2 depends upon its CO_2 and Nitrogen Growth Environment

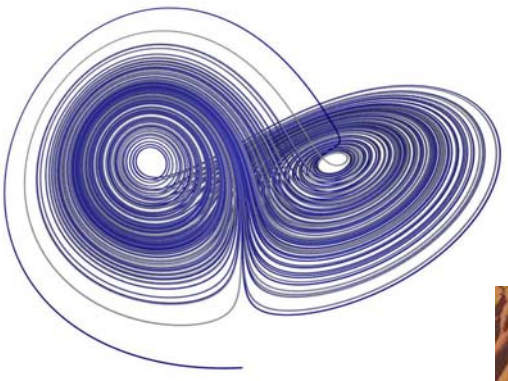


Ainsworth and Rogers 2007, PCE; adapted from Bloom, 2009 Cal Ag

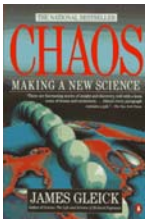
- Complexity is not the same as Random, it is **Deterministic**
- Simple sets of Coupled Ecological or Meteorological Differential Equations (dx/dt=f(x)) can produce Complex Behavior
  - Lord Robert May, Nature, 1974
  - Ed Lorenz, J. Atmos Sci, 1963

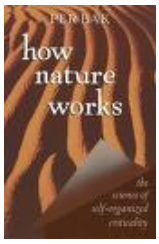
Complexity:
Creating Order out of Chaos and Establishing the Limits on Predictability





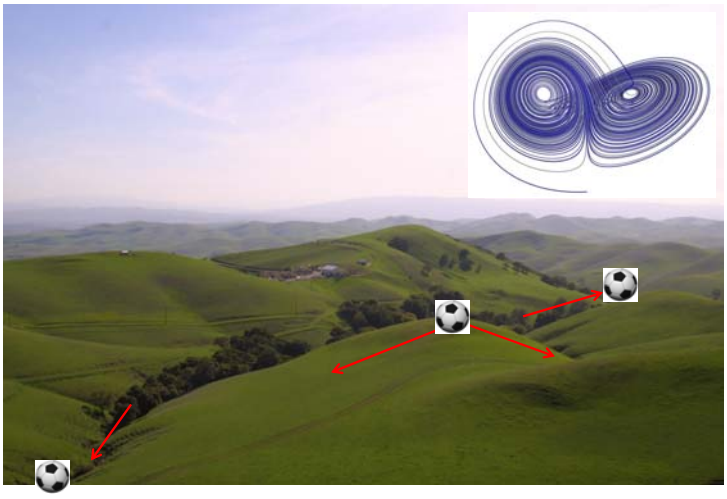
Lorenz Attractor



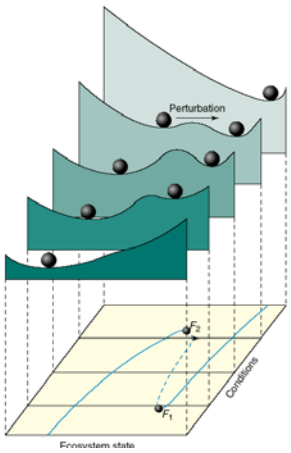


Example of Self-Organization
Polygons in the Tundra

Sensitivity to Initial Conditions and Path Dependence



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

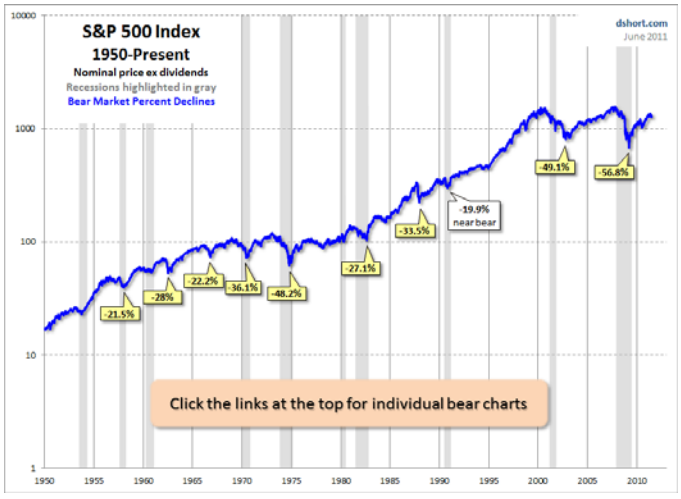


A Lesson and Warning for Unintended Consequences, when Perturbing Complex Systems

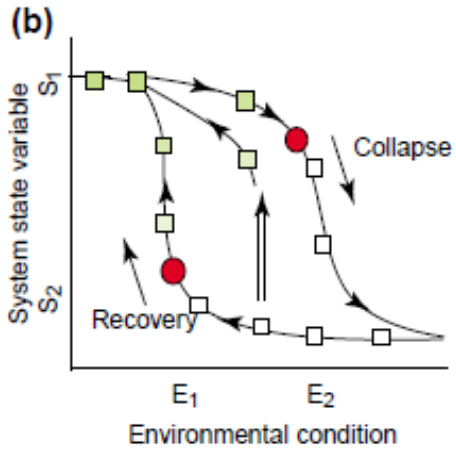
An Example of the Delicate balance between Stability and Collapse

Scheffer and Carpenter, 2003 TREE

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

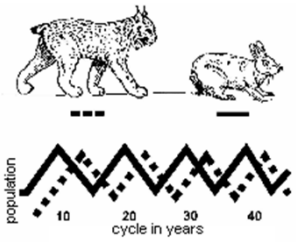


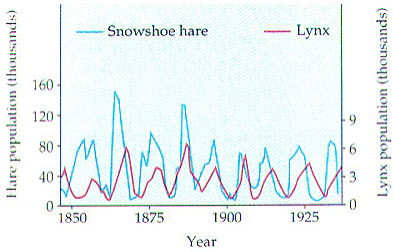
Hysteresis—another non-linear response--in Ecology



Suding et al 2004 TREE

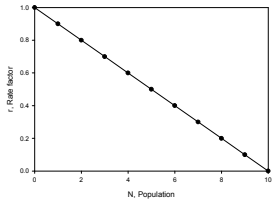
Chaos and Complexity in Predator-Prey Dynamics





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

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



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

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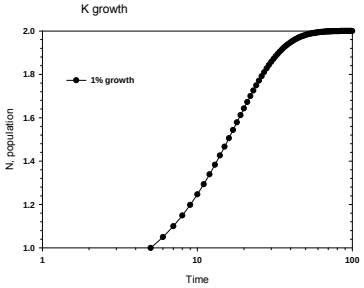
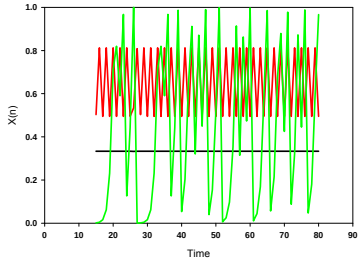
$$\frac{dN}{dt} \approx \frac{\Delta N}{\Delta t} = N \cdot r(N) = N\, r(1 - \frac{N}{K})$$

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





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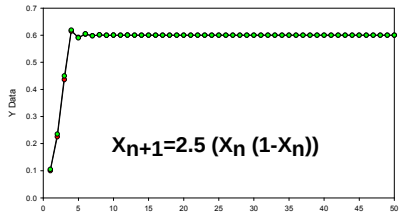
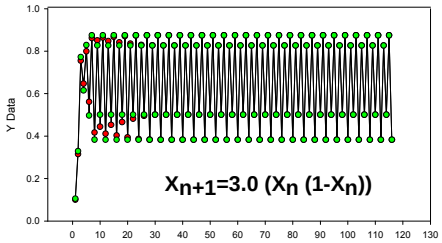
Steady state, r < 3

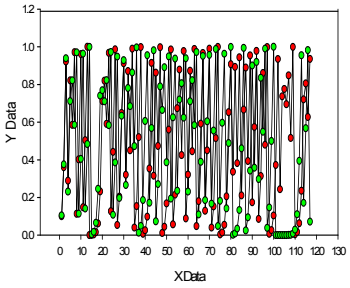


Chaos Examples and sensitivity to initial conditions

Period doubling, 3 < r < 3.5



Chaos, r > 3.5



$X_{n+1}=4.0\ (X_n\ (1-X_n))$

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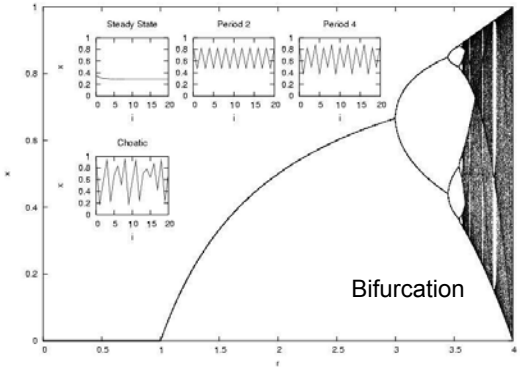
Chaos from a Recursive Equation $X_{n+1} = r\ x_n(1-x_n)$



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

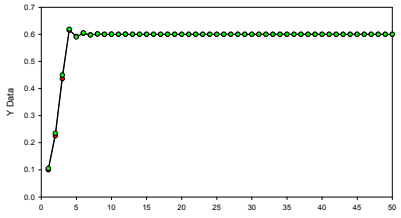
- Ecosystems are Complex Adaptive systems
- Ecosystems work across a hierarchy of time and space scales that span over 14 Orders of Magnitude
- Ecosystems are Resilient to small Perturbations
- Ecosystems are Vulnerable to Switching States, if Pushed too Hard, and may Experience Hysteretic Response on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

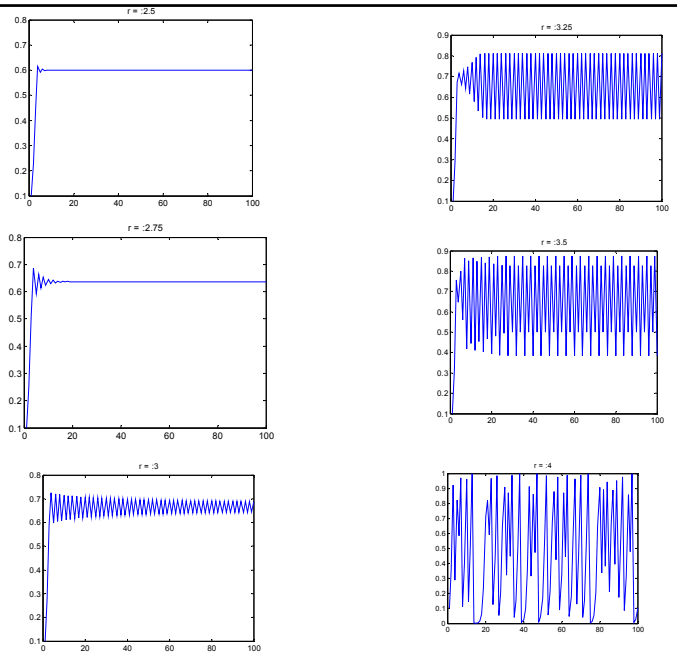
Discussion Material

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

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





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

Ecological Stoichiometry, CO_2-H_2O-N-P
$C_{106}H_{263}O_{110}N_{16}P$

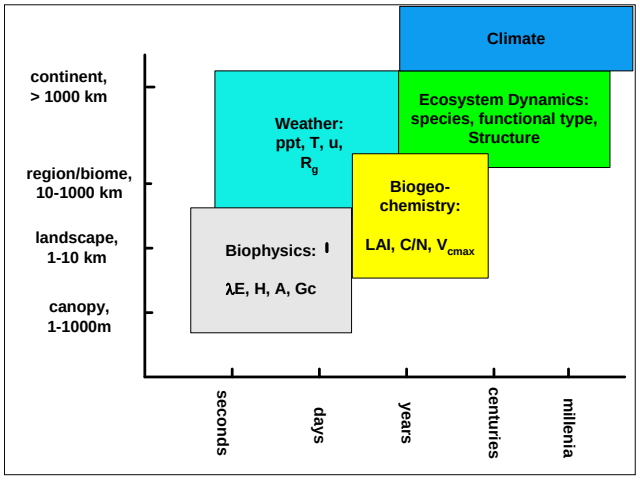
- CO_2
  - Primary source of high-energy sugars, CH_2O
- Nitrogen
  - Key component in RUBISCO, the enzyme that fixes CO_2, and amino acids that form proteins
- Phosphorus
  - Key component of ATP and NADPH, the energy compounds central to many metabolic processes
- H_2O
  - Keeps cells turgid
  - Solvent for transferring nutrients through solution
  - Lost via stomata

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

Process and Rates are a Matter of Scale, too



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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
  - Hierarchal Structure
  - Scale Emergent Processes
  - Heterogeneity of components
  - Flows of material and Energy

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

ESPM 111 Ecosystem Ecology

Scale-Emergent Properties

- Whole ≠ 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 CO_2
    - Leaf Photosynthesis increases non-linearly with CO_2
    - 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
  - 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

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.