Ecosystem Ecology: History

- Objectives:
  - Overview of people and events important in the development of ecosystem ecology as a discipline
  - Historical context of ecosystem ecology as a discipline

Ecosystem Ecology: History

- Why should we care about historical context?
  - Helps understand ecosystem ecology
    - How it came about as a discipline within ecology
    - How it fits in with other disciplines inside (e.g., population and community ecology) and outside (e.g., geology; climatology) of ecology
  - Further reading
    - Golley, F. B. 1994. *A history of the ecosystem concept in ecology: More than the sum of the parts*. Yale University Press, Newhaven and London. 254 pp.

Ecosystem Ecology: History

- How old is ecosystem ecology as a field of study?
  - Ecology is a relatively young discipline (~120 yrs)
    - 1st Ecology class taught by Henry Cowles at the University of Chicago in 1897
    - Sir Arthur Tansley taught 1st Ecology course in England in 1899
  - Ecosystem Ecology is ~75 yrs old
    - Sir Arthur Tansley 1st to use the term "<u>ecosystem</u>" in 1935

Ecosystem Ecology: History

- Ecosystem Concept resulted from the synthesis of 3 different sets of ecological ideas
  - (1) Succession (Midwestern Botanists)
    - Ecological context: *sequence of vegetation development over time*
    - Ecosystem context: *directional change in ecosystem structure and function resulting from biotic-driven changes in resource supply*
    - Primary vs. Secondary succession
      - 1°: occurs on “barren land”; no soil and no *in situ* source of plant propagules; very small fraction of Earth’s surface
      - 2°: occurs following disturbance on land with soil and some plant propagules *in situ*; majority of Earth’s surface

Ecosystem Ecology: History

- Succession
  - Henry Cowles (1869-1939)
    - University of Chicago
    - Vegetation change (i.e., succession) over time on Lake MI sand dunes in response to physical stresses
    - Orderly developmental sequence of vegetation change against backdrop of unpredictable physical disturbance
    - Plant communities are dynamic, stochastic, and ever-changing

Ecosystem Ecology: History

- Succession
  - Frederic Clements (1874-1945)
    - University of Nebraska and the Carnegie Institute of Washington
    - Succession is a linear process to a predictable ‘climax community”
    - Community is analogous to an organism
      - Made up of interacting parts, with its own physiology and evolution
    - Took the analogy to the extreme: believed that communities really were organisms

Ecosystem Ecology: History

- Succession
  - Henry Gleason (1882-1975)
    - University of Michigan
    - Big critic of Clements
    - Individualistic concept of plant communities
      - Community is an assemblage of individuals
      - Climax community is not predictable
      - Each species has a unique range of environmental tolerances
      - Seed dispersal is completely random
    - Therefore, a community is a result of chance migration and selection by the environment, and is at least somewhat unpredictable

Ecosystem Ecology: History

- Ecosystem Concept resulted from the synthesis of 3 different sets of ecological ideas
  - (2) Trophic Interactions (Animal ecologists & limnologists)
    - Feeding relationships among organisms (pyramid)
    - Trophic interactions play a very strong role in structuring communities

Ecosystem Ecology: History

- Trophic interactions
  - Charles Elton (1900-1991)
    - Oxford University
    - Laid groundwork for trophic dynamics
      - Niche: role of an animal in a comm. (what it eats and who it is eaten by)
      - Food chain (pyramid): links different niches; fundamental organizational unit of all communities; food chain forms a pyramid where each successive level has fewer, larger animals
      - Food cycle: complex trophic interactions
    - Focused on transfer of matter, not energy; but laid groundwork for studies of energy transfer thru ecosystems

Charles Elton setting mouse traps in Bagley Wood, near Oxford, in 1926.

Ecosystem Ecology: History

- Ecosystem Concept resulted from the synthesis of 3 different sets of ecological ideas
  - (3) Biogeochemistry (Limnologists & Geochemists)
    - Study of the cycles of chemical elements (e.g., C and N) and their interactions with and incorporation into living things
      - Biologically driven chemical processes, and/or those chemical processes that impact biological activity
    - Cycling of energy and materials into, within, and out of ecosystems
      - Influenced by, or impact on, biota

Ecosystem Ecology: History

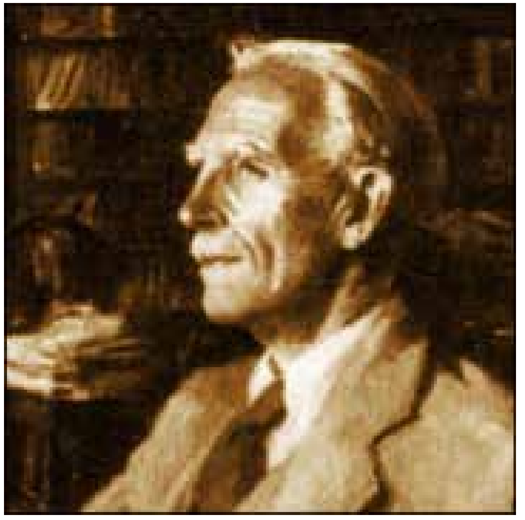
- Biogeochemistry
  - G. Evelyn Hutchinson (1903-1991)
    - Yale University (& many of his students)
    - Father of modern limnology
      - Studied history of aquatic productivity and chemistry in lake sediments
      - Combined work on biogeochemistry and population biology
    - Early proponent of use of mathematical models to describe ecological processes
      - Systems analysis (systems science, systems ecology)

Ecosystem Ecology: History

- Biogeochemistry
  - Vladimir Sukachev: 1880-1967
    - Russian botanist
    - Founder of biogeocoenology (biogeocoenosis)
      - *"A complex of homogenous components (atmosphere, bedrock, soil and hydrological conditions, vegetation, fauna and microorganisms), which has special interactions and substance and energy exchange between these components and with other natural phenomena. It represents an ever developing dialectic unit".*
    - Early proponent of ecosystem ecology and biogeochemistry, but his writing was buried for decades in obscure Russian literature

Ecosystem Ecology: History

- "Ecosystem" coined in 1935
  - Sir Arthur Tansley (1871-1955)
    - British Plant Ecologist, Co-founder of *British Ecological Society*, & Editor of *Journal of Ecology* for 20 yrs
    - Supporter and critic of Clements
      - Embraced certain aspects of organismal analogy, but thought it went too far
    - Ecosystem was an alternative concept
      - "*including not only the organism-concept, but also the whole complex of physical factors forming what we call the environment of the biome*"
      - Biotic AND abiotic components considered



Ecosystem Ecology: History

- The synthesis
  - Succession, trophic dynamics, and biogeochemistry
    - 1st realized by the limnologist Ray Lindeman
    - Influenced by succession ideas of Cowles, Clements, and Tansley
    - Ph.D. student at University of Minn.
      - Trophic dynamics of Cedar Bog Lake
    - Postdoc at Yale with G.E. Hutchinson
      - Biogeochemistry and mathematical models of energy flow

Ecosystem Ecology: History

- *The trophic-dynamic aspect of ecology*
  - 1942, Ecology: Vol. 23, No. 4, pp. 399-417

  1. Succession: expanded earlier work to include energy–how does productivity change during succession? (not just how the organisms change)

  2. Trophic theory: expanded Elton's ideas to distinguish flow of matter vs. energy
    - Matter is continuously recycled vs. energy flows one-way
    - Energy lost as heat as matter is transferred through trophic cycle, so one-way transfer of energy must always be replenished

  3. Biogeochemistry: integrated abiotic and biotic systems into mathematical models

Ecosystem Ecology: History

- *The trophic-dynamic aspect of ecology*
  - 1st submission rejected at *Ecology*
  - Lindeman died at age 27 of liver failure
  - Published posthumously in 1942 after intervention by Hutchinson
    - Considered one of, if not the single, most important papers on energy flow in ecosystems
    - Cited >2,250 times to date

Ecosystem Ecology: History

- Ecosystem ecology as an organizing concept
  - Ecosystem concept has been an organizing theme in ecology for >50 years
  - Eugene Odum: published “Fundamentals of Ecology” in 1953 with an ecosystem and systems analysis focus (nutrient cycling and energy flow)
  - “Ecophysiology” provided many of the mechanisms for observed patterns
    - Interrelationships between the physiology of organisms and their environment

Ecosystem Ecology: History

- Events:
  - 1950s
    - National Science Foundation (NSF) formed to support basic research in all fields of science
    - AEC formed to use radioactive tracers to follow materials through ecological systems
      - Provided a perfect “test bed” for testing and developing theory and principles in ecosystem ecology

Ecosystem Ecology: History

- Events:
  - 1960s
    - Lots of focus on ecosystem productivity (Robert Whittaker)
    - Hubbard Brook Experiment Begins (Bormann and Likens)
      - Outdoor laboratory for ecological studies in the White Mountains of New Hampshire
      - Initially established to study the relationship between forest cover and water quality/quantity
    - Mathematical modeling of ecosystems begins in earnest
    - International Biological Program (IBP) Founded at NSF
      - Decade long effort to coordinate large-scale ecological and environmental studies in an attempt to address pressing environmental issues (within the context of ecosystem ecology)

Ecosystem Ecology: History

- Events:
  - 1970s
    - Formation of “Ecosystem Studies” program in the Division of Environmental Biology (DEB) at NSF
    - Peter Vitousek begins career
    - Formation of Long-Term Ecological Research (LTER) program at NSF
      - Ecosystem Studies and LTER now run jointly under the Ecosystem Science Cluster

Ecosystem Ecology: History

- Events:
  - 1980 to present
    - Advent of landscape ecology and spatial analysis
    - Wealth of journals and books
    - Change in focus
      - Homogeneous → Heterogeneous
      - Natural → Managed
      - Descriptive → Manipulations to identify mechanisms
    - Large collaborations across multiple disciplines
    - Science → Policy
    - NSF National Ecological Observatory Network (NEON)
      - …*continental scale research instrument consisting of geographically distributed infrastructure, networked via cybertechnology into an integrated research platform for regional to continental scale ecological research*.

Ecosystem Ecology: Concept

- Objectives:
  - Introduce the ecosystem concept
    - What is it?
      - Current thought and use
    - How does it fit in with other disciplines?
    - Why is it important in today's world?

  - Additional Reading:
    - Currie WS (2011) Units of nature or processes across scales? The ecosystem concept at age 75. *New Phytologist*, 190, 21-34.
    - Gignoux J, Davies I, Flint S, Zucker J-D (2011) The ecosystem in practice: Interest and problems of an old definition for constructing ecological models. *Ecosystems*, 14, 1039-1054.

Ecosystem Ecology: Concept

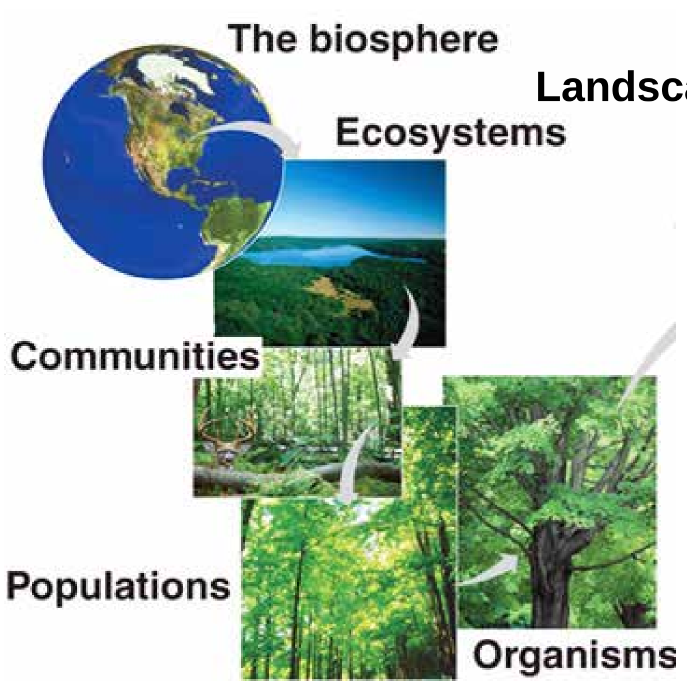
- What is ecosystem ecology?
  - "*study of interactions between organisms and their physical environment as an integrated system*"
    - Fundamental for sustainable management of natural resources
      - Provides the link between biotic and abiotic systems
      - Incorporates humans & their activities
    - Provides information needed to understand the consequences of societal choices
  - How does this differ from ecology?
    - "*the study of the distribution and abundance of living organisms, and their interactions with each other and their physical environment*"

Ecosystem Ecology: Concept

- What is an ecosystem?
  - *Bounded ecological system consisting of all the organisms in an area and the physical environment with which they interact*
    - Biotic and abiotic processes are implicitly considered
      - Response of organisms to their environment <u>&</u> effects of organisms on their environment
  - Energy is a central theme in the ecosystem concept
    - Ecosystem: "*an energy-driven complex of a community of organisms and its controlling environment*" (Billings 1978)

Ecosystem Ecology: Concept

- Where do ecosystems fit into the ecological hierarchy?



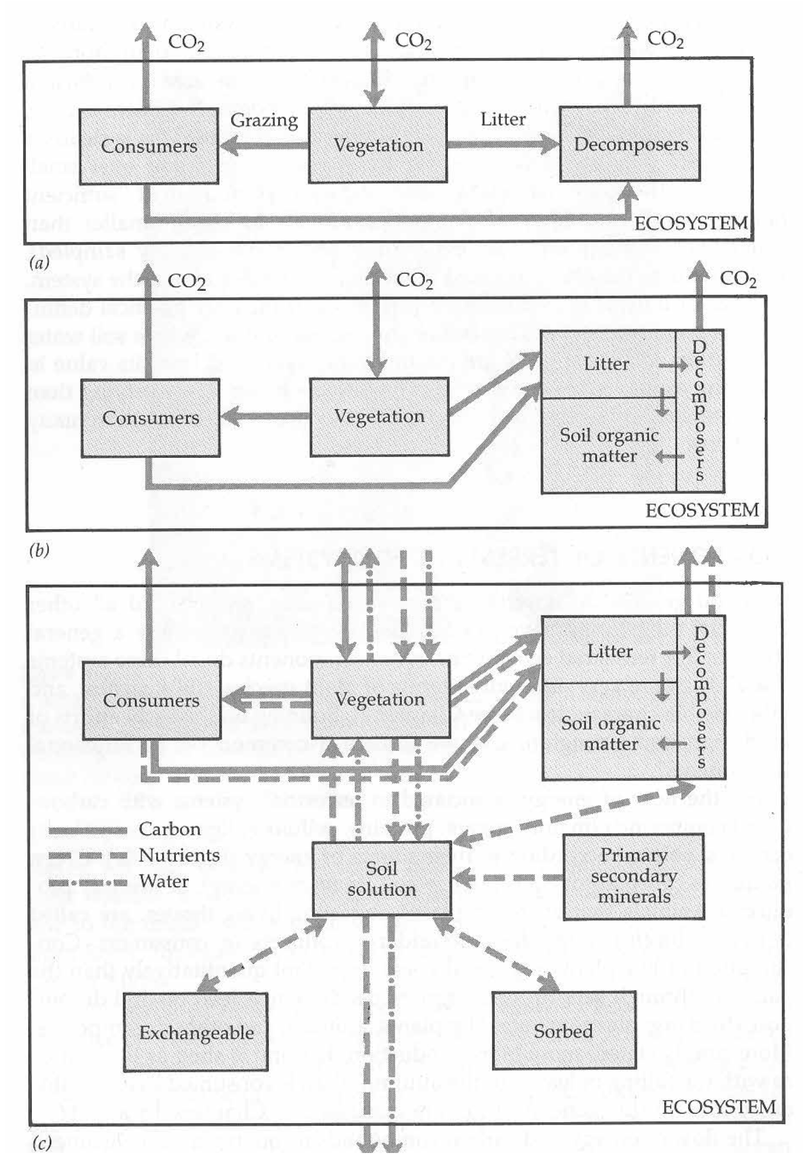
(Individuals)

Landscapes

Simple ecosystem model

Pools (boxes) = <u>quantity</u> of energy or material in an ecosystem compartment

Fluxes (arrows) = <u>flow</u> of energy or materials from one pool to another (≈ ecosystem processes)



C

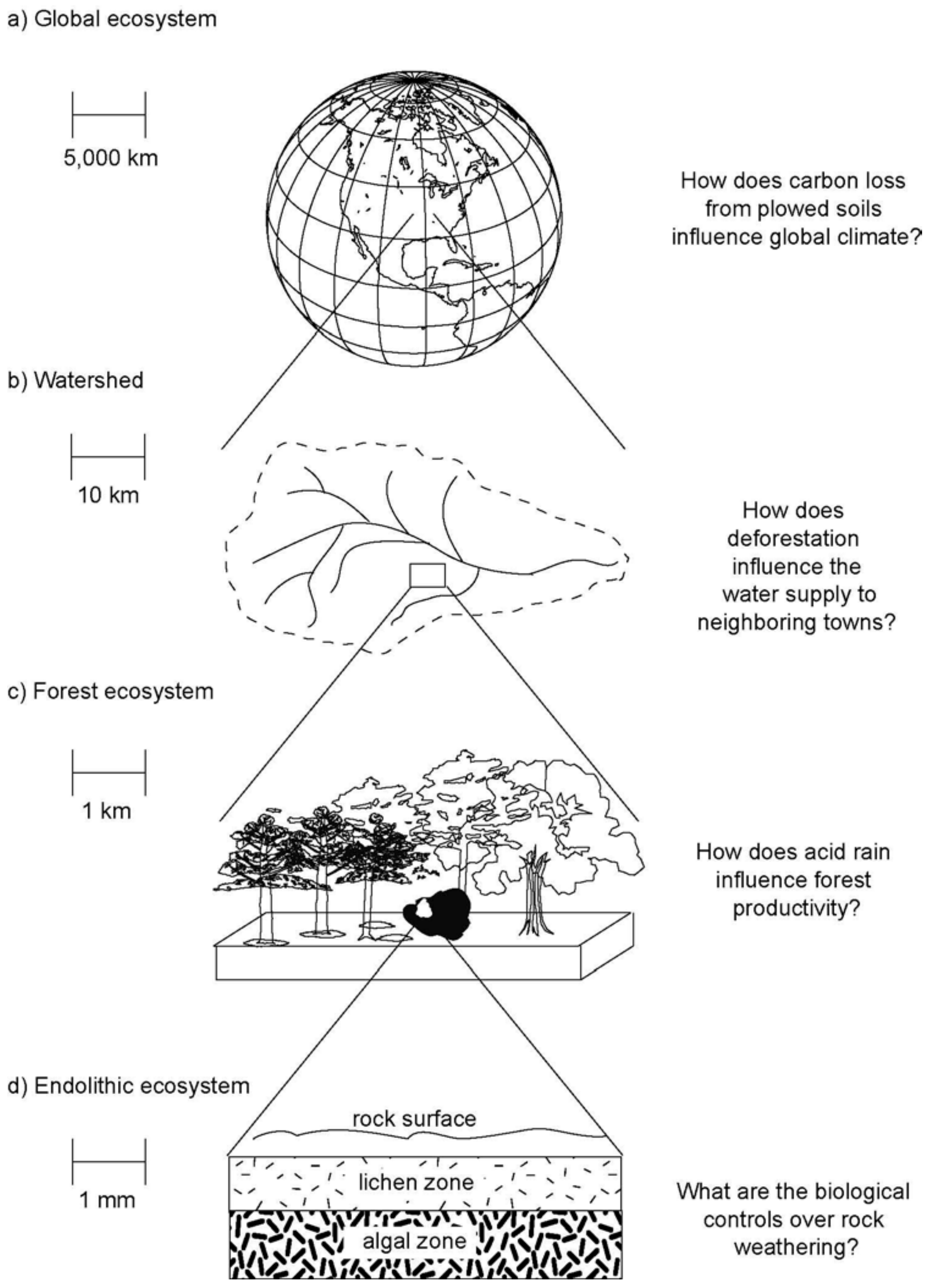
C

C, Nutrients & H_2O

Aber & Melillo 1991

Spatial scale

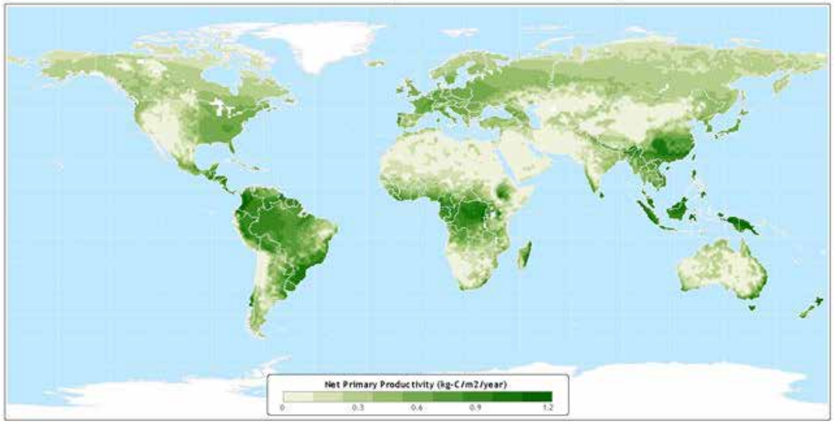
- Distribution in space
- At what spatial scale are ecosystems defined?



Spatial scale

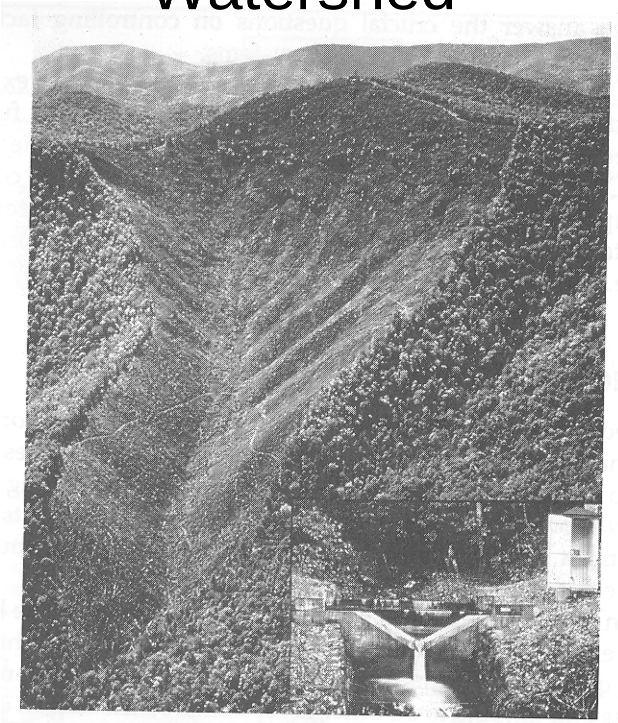
Globe

Net Primary Productivity



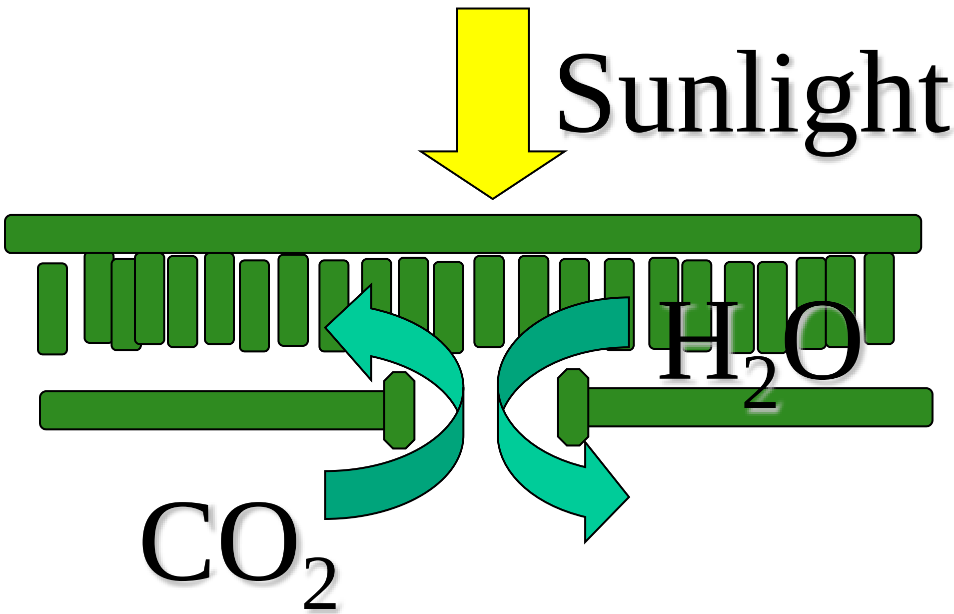
Forest Stand

Watershed



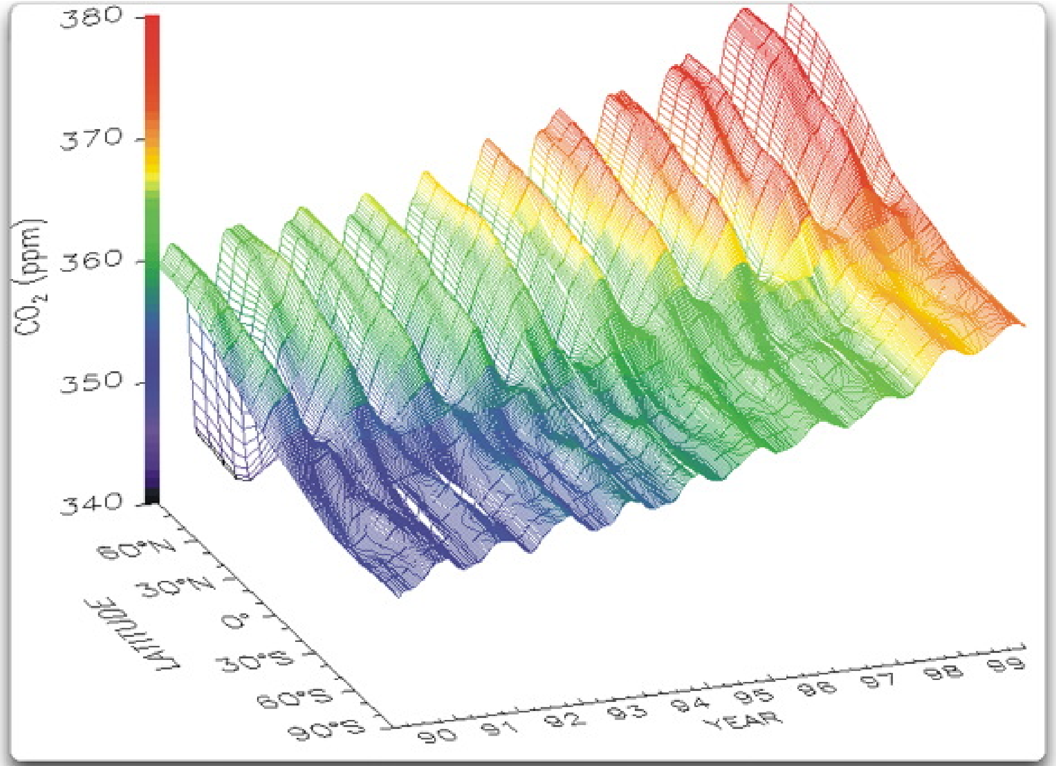
Temporal Scale (Distribution in Time)

- Instantaneous (sec)



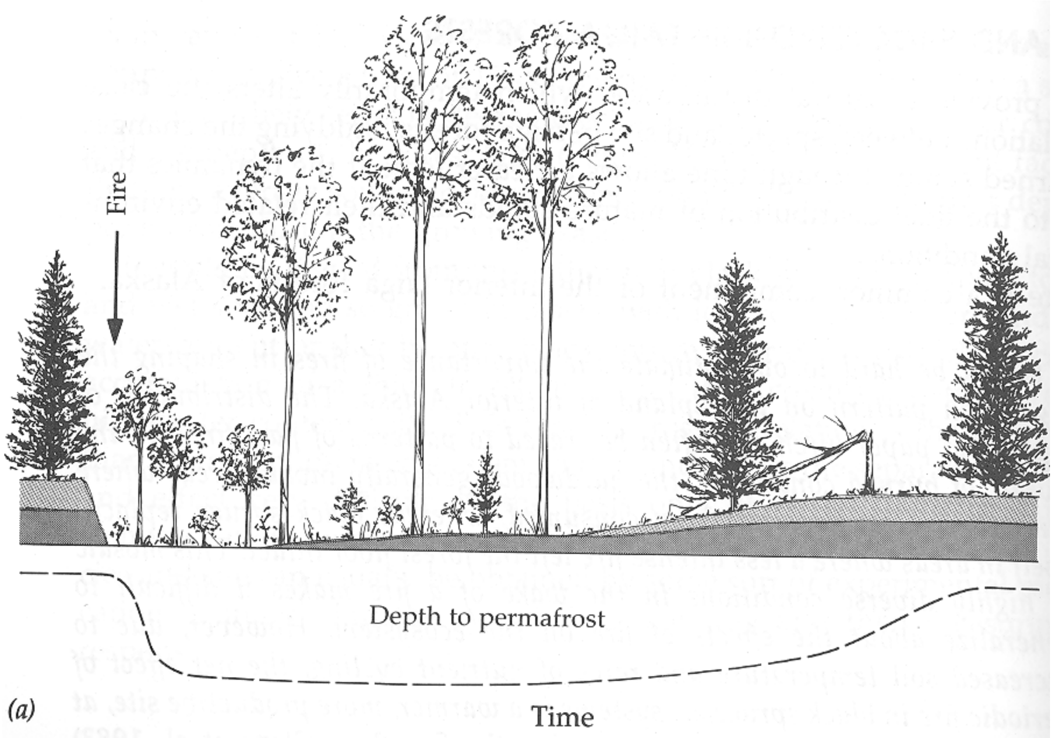
Temporal Scale

- Instantaneous (sec)
- Seasonal (yr)



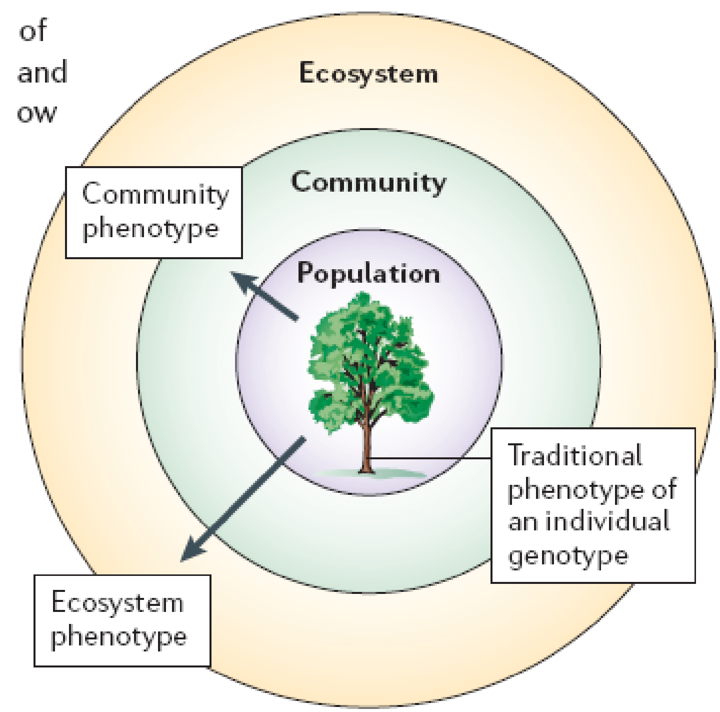
Temporal Scale

- Instantaneous (sec)
- Seasonal (yr)
- Successional (10 to 100s yrs)



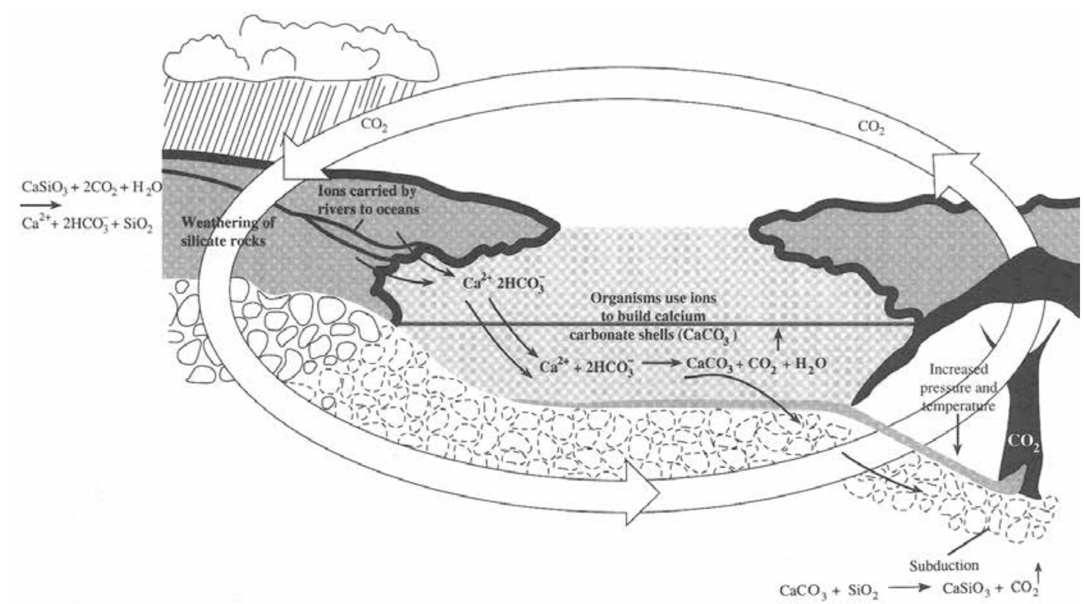
Temporal Scale

- Instantaneous (sec)
- Seasonal (yr)
- Successional (10 to 100s yrs)
- Evolutionary (100s to 1000s yrs)
  - Natural selection controls inter- and intraspecific variability in ecosystem processes



Temporal Scale

- Instantaneous (sec)
- Seasonal (yr)
- Successional (10 to 100s yrs)
- Evolutionary (100s to 1000s yrs)
- Geologic (1,000s to 1,000,000s yrs)



Temporal Scale

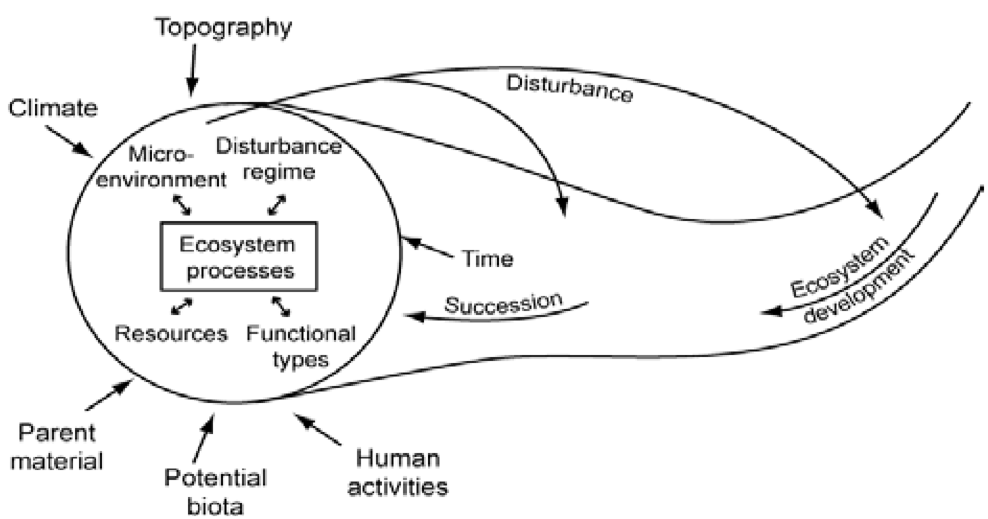
- Shift from viewing ecosystems as static (equilibrium) to dynamic (nonequilibrium)
  - Unbalanced inputs/outputs
  - External and internal forcing factors
  - No single stable state
  - Disturbance is the norm
  - Legacy of past events
  - Human activities exert pervasive influence
- Steady state → balance between inputs and outputs shows no trend over time
  - Acknowledges temporal and spatial variation as normal
  - "Balance" does not mean that inputs = outputs, but rather that there is no change in the balance over time

How do you characterize an ecosystem?

- Structure
  - Physical and spatial distribution of components
    - Horizontal and vertical distribution of species/pop./comm.
    - Biotic components (biodiversity, composition)
      - Plants – Decomposers – Consumers
    - Abiotic components
      - Water, atmosphere, soil, parent material
- Function (Processes)
  - Ecological processes that maintain structure
    - Energy and material flow/transfers
      - Autotrophs (plants) vs. heterotrophs (decomposers & consumers)
    - Biogeochemical cycles
      - Biogeochemistry: biologically influenced chemical processes in ecosystems (C, N, P, S, K, Ca, H_2O, etc.)
      - Incorporates biological, geological, and chemical aspects of processes and reactions that govern the composition of the natural environment
      - Importance of <u>coupled</u> biogeochemical cycles

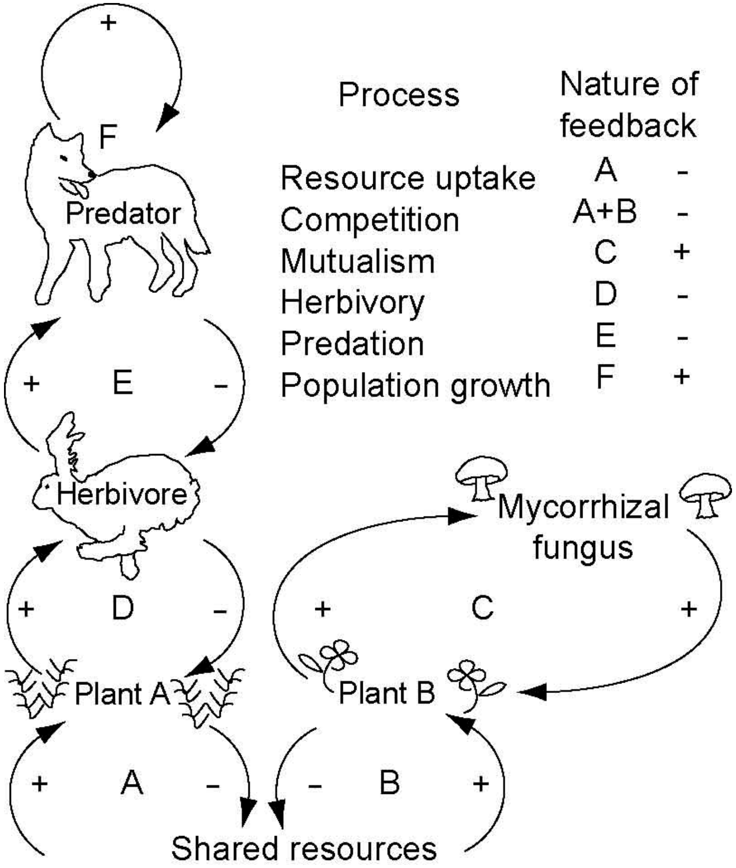
Ecosystem structure and function

- What controls ecosystem processes (structure & function)?
  - 5 independent state variables
    - Set the bounds for the characteristics of a given ecosystem
      - Same 5 state variables that control soil formation (Hans Jenny, 1941)
    - These factors control but are not controlled by ecosystems
  - Human activities as a 6th state variable
  - Also at least 4 “interactive controls”
    - Factors that both control and are controlled by ecosystem characteristics



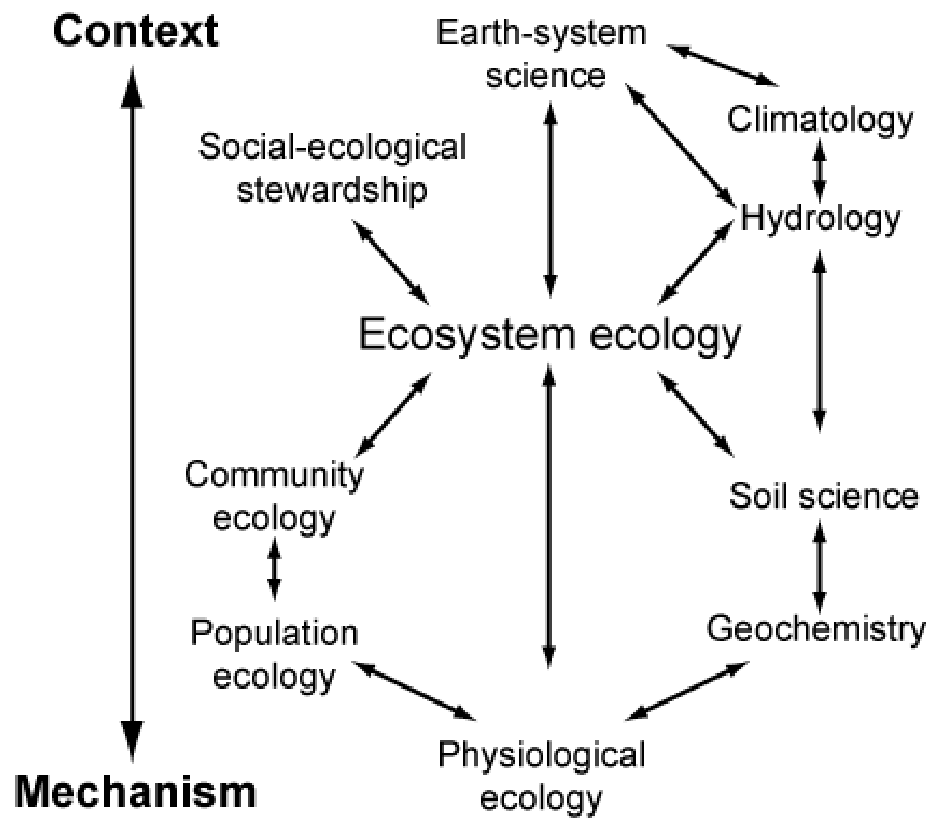
Ecosystem Feedbacks

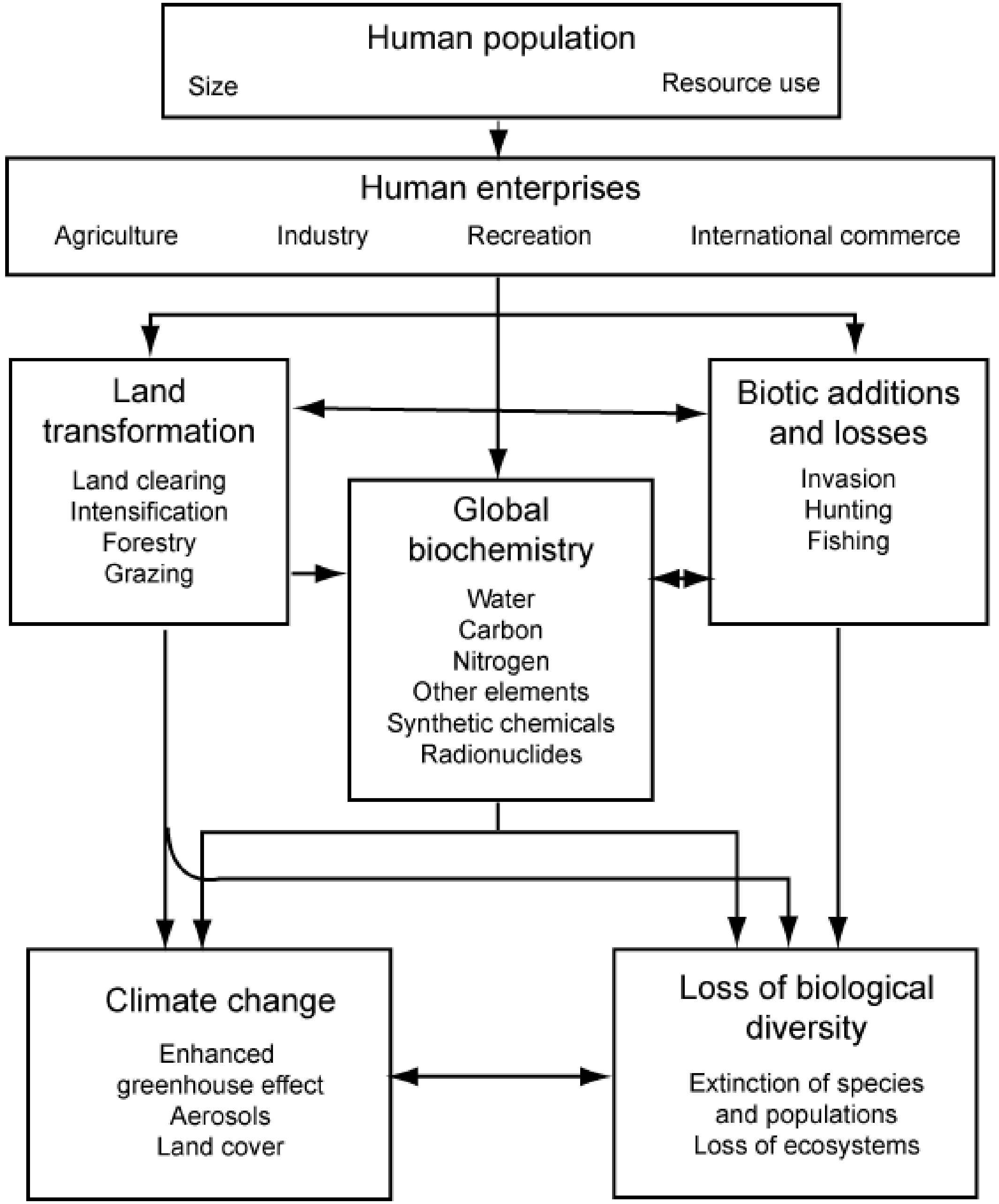
- Feedbacks regulate the internal dynamics of ecosystems
  - Can be negative (stabilizing) or positive (amplifying)
    - Negative feedbacks act as a balance to maintain ecosystems in current state
      - Negative when 2 components have opposite effect on each other
    - Provide stability in the face of change, where stability is a function of:
      - Resistance (ability to resist change)
      - Resilience (ability to return to pre-existing conditions)
  - Threshold: critical level of one or more ecosystem controls that, when crossed, causes abrupt ecosystem change



Ecosystem Ecology Integrates Across Multiple Disciplines

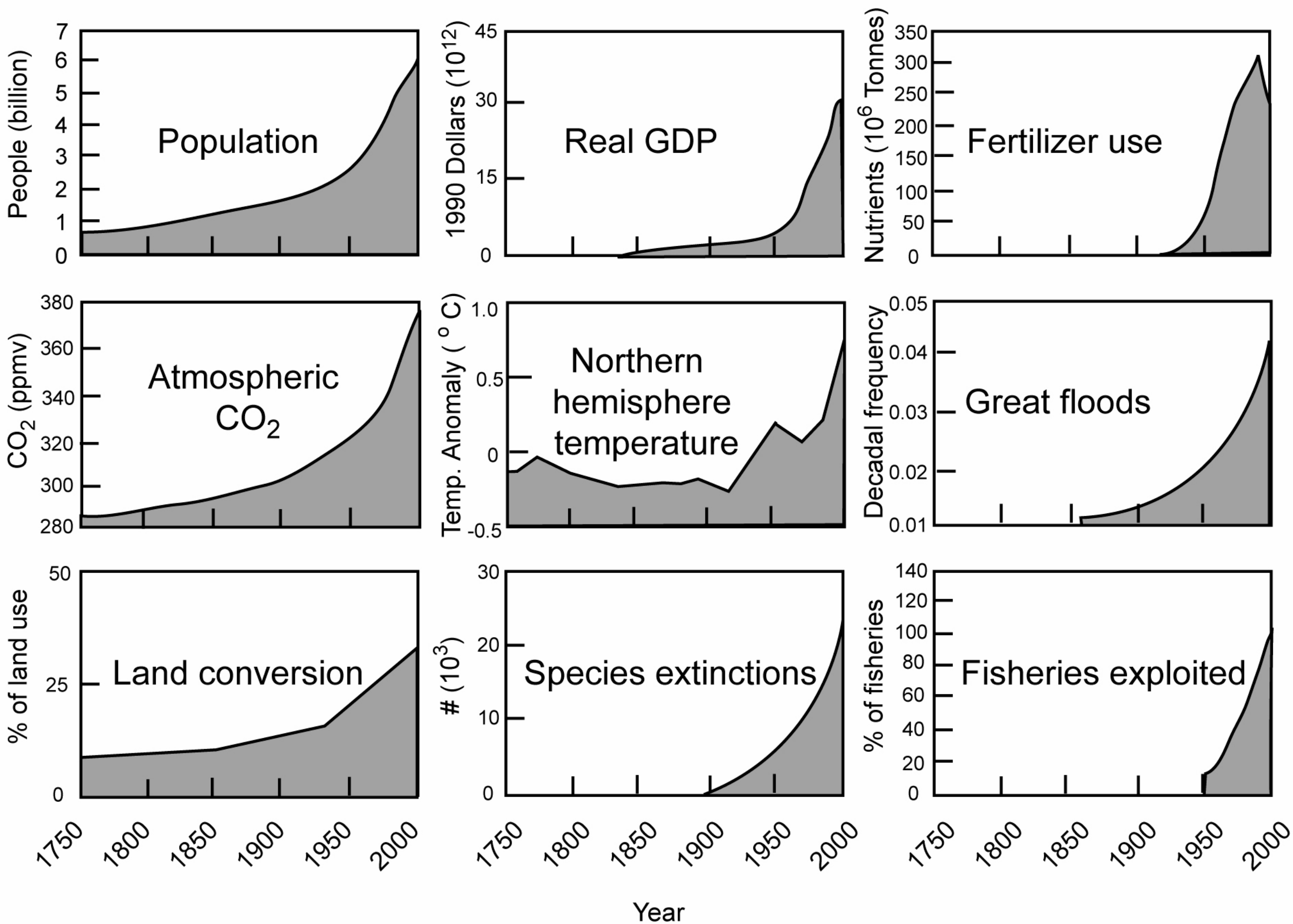
- Why should we care about ecosystem ecology?
  - Provides a mechanistic basis for understanding the Earth System
    - Ideal for management of Earth's resources
    - Increased emphasis on ecosystem goods and services
    - Human activities are drastically and rapidly changing ecosystems and, therefore, the Earth System

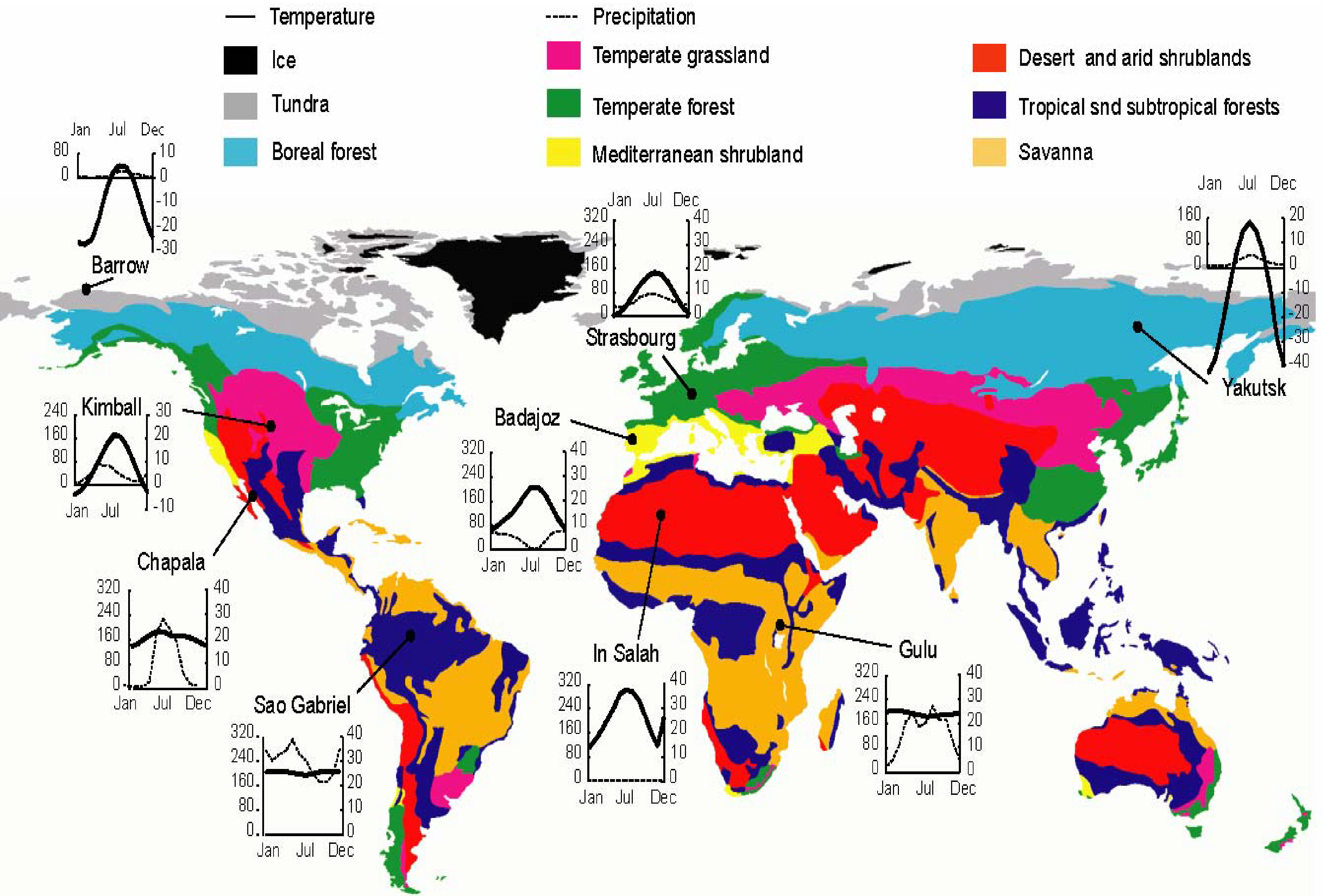




Vitousek et al. 1997

"Human exploitation of Earth's ecosystems has increased more in the last half century than in the entire previous history of the planet."





Temperature
Precipitation
Ice
Tundra
Boreal forest
Temperate grassland
Temperate forest
Mediterranean shrubland
Desert and arid shrublands
Tropical snd subtropical forests
Savanna
Barrow
Kimball
Chapala
Sao Gabriel
Badajoz
Strasbourg
In Salah
Gulu
Yakutsk
Jan
Jul
Dec