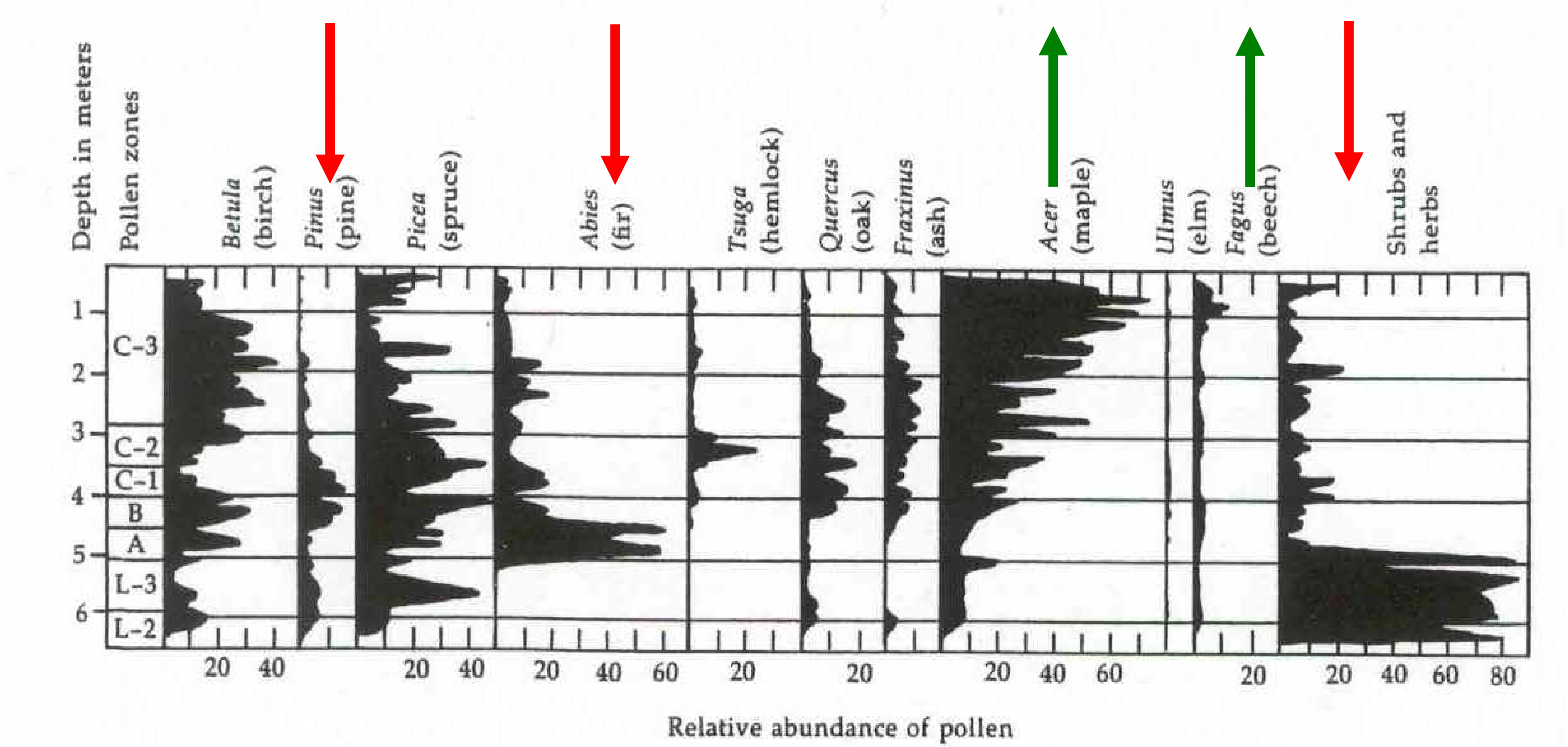
Temporal and spatial dynamics

- Objectives
  - Change in ecosystem structure and function with time (**temporal**) and across the landscape (**spatial**)
    - Inherent, natural ecological change (vs. human-induced change)
    - Primarily in response to changes in abiotic environmental drivers

Temporal and spatial dynamics

- Ecosystems are always "recovering" from something
  - 9,000 yr pollen record from Northern temperate forest

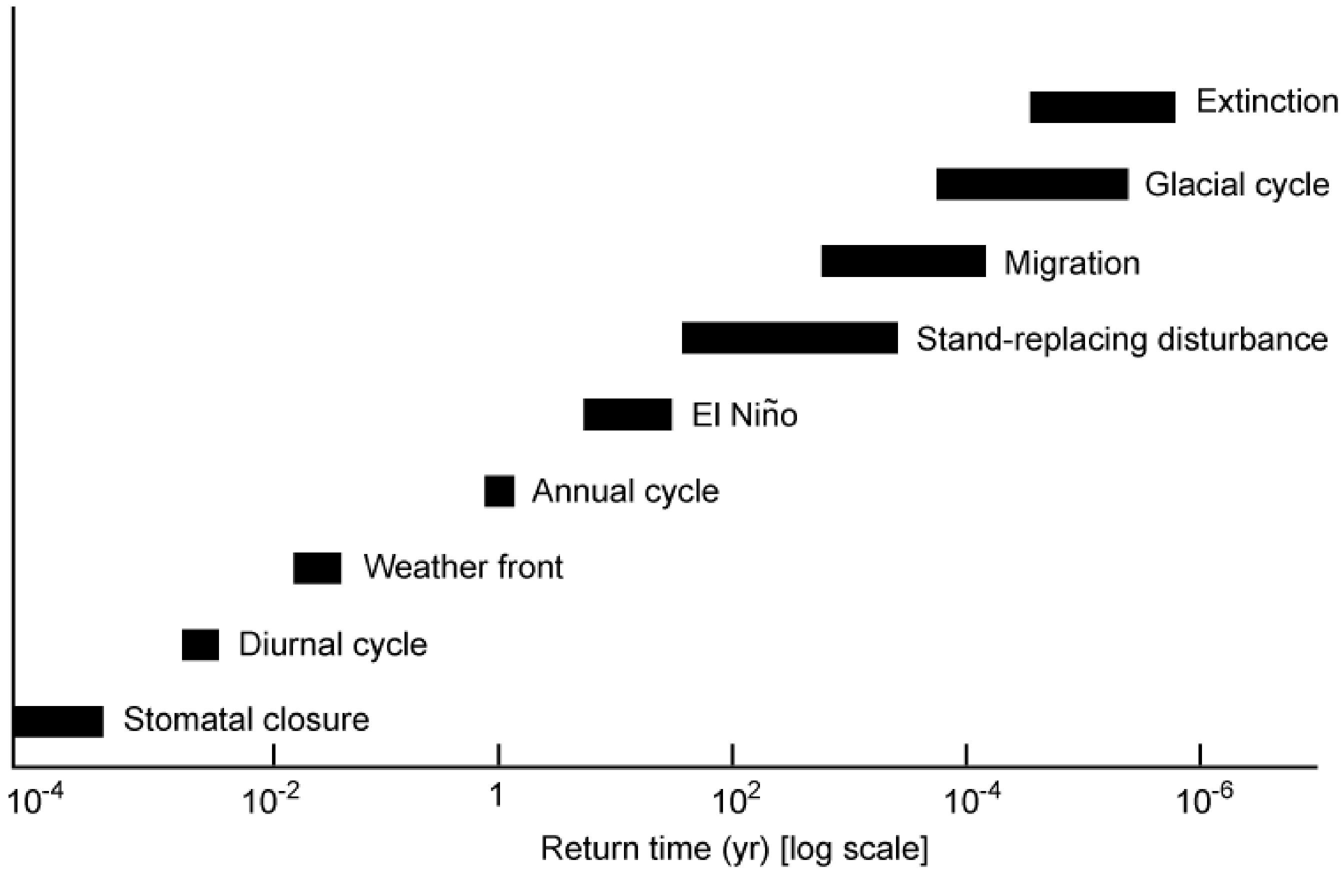


Temporal and spatial dynamics

- Ecosystems are always “recovering” from something
  - Influenced by both current and past physical environment, and disturbances
    - Historical legacies
  - Typically not in equilibrium with current environment
    - Time lags
    - No-analog communities
  - Concept of “steady state” implies equilibrium, and no directional change in ecosystem properties over time
    - Likely not reasonable assumptions for most/all ecosystems

Temporal and spatial dynamics

- Temporal scale is critical in determining how ecosystem properties change over time



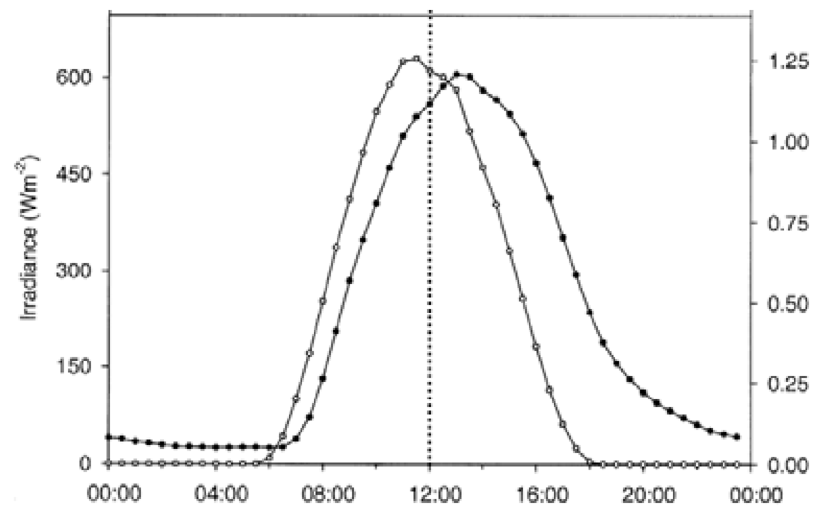
Temporal and spatial dynamics

- Temporal scales that influence ecosystem processes
  - Instantaneous (sec)
  - Diel (24 hours)
  - Seasonal (yr)
  - Interannual (2-10 Years)
  - Successional (10 to 100s yrs)
  - Evolutionary (100s to 1000s yrs)
  - Geologic (1,000s to 1,000,000s yrs)

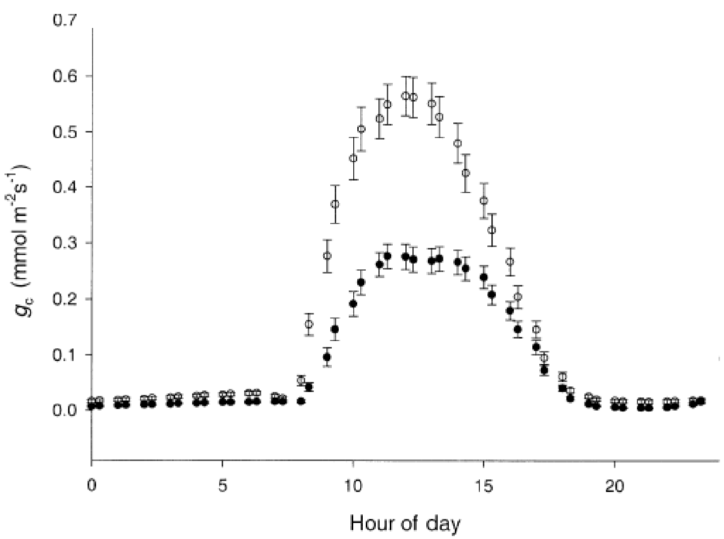
Temporal and spatial dynamics

- Diel fluctuations
  - Photosynthesis greater in morning than afternoon
    - Even if environment stays the same
    - Plants are larger C sinks in the morning
  - Transpiration tends to peak at midday when irradiance and VPD peak

Temporal and spatial dynamics



O'Brien et al. 2004



- 2 species
- 90 day averages

Temporal and spatial dynamics

- Seasonal fluctuations
  - Plants grow rapidly in spring
    - Resources readily available, physical environment is at an optimum, etc.
  - Plants senesce in autumn
    - Commonly in response to photoperiod (or temperature)
  - Wet-dry seasonality in subtropics and tropics
    - Beginning and ending of rainy season very distinct environmentally
    - Drought-deciduous species

Temporal and spatial dynamics

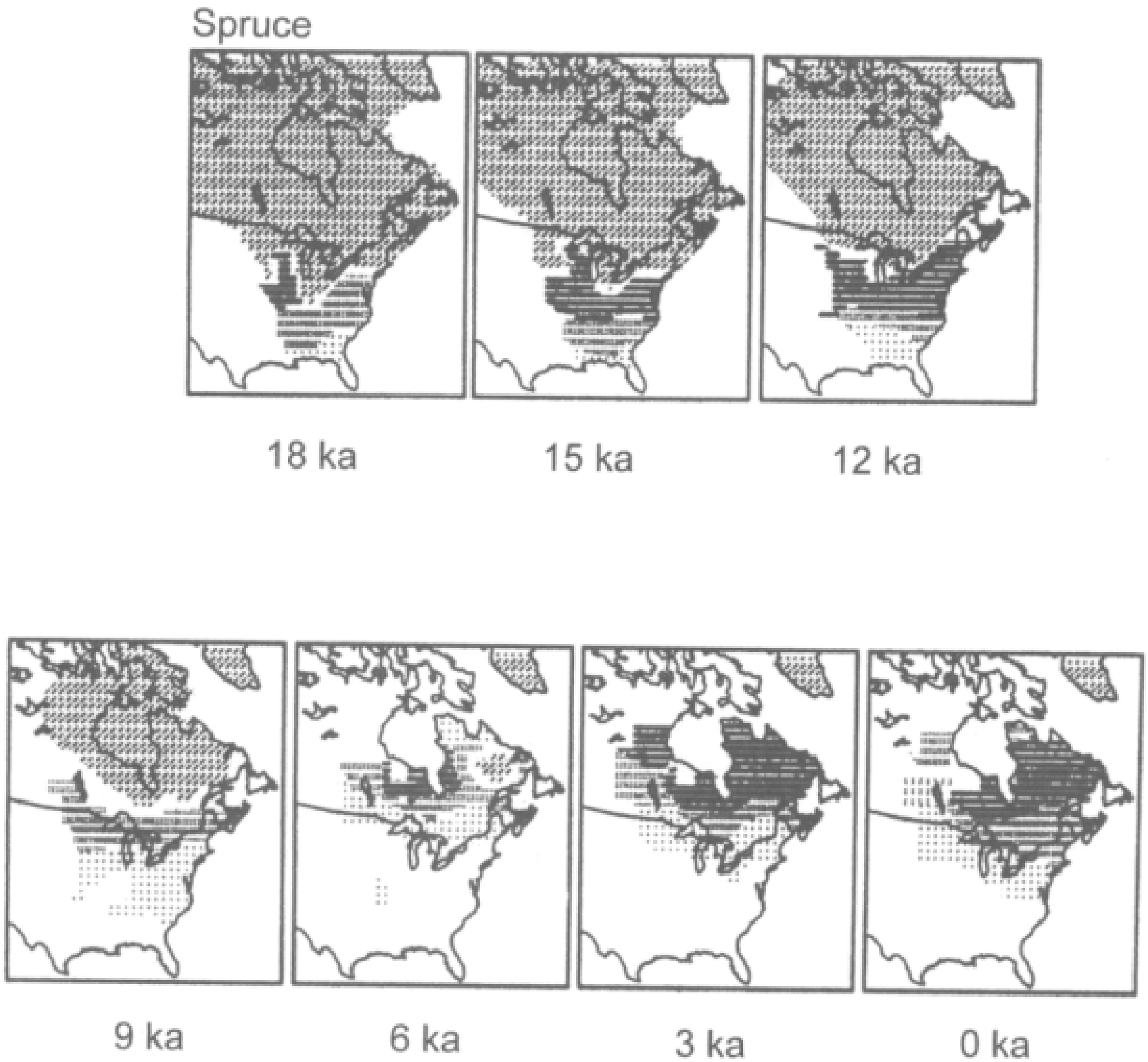
- Interannual fluctuations
  - Environment
    - e.g., ENSO, Northern Atlantic Oscillation, Pacific Decadal Oscillation, etc.

Temporal and spatial dynamics

- Longer-term changes & legacies
  - Climate change
    - Vegetation responds slowly
      - Post-glacial migration
      - Time lags
      - No-analog communities
  - If plant communities lag behind climate, soils lag even further
    - Soils (belowground resources) are the primary interactive control over most ecosystem process rates

Temporal and spatial dynamics

- C



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Millar & Brubaker (2006)

Temporal and spatial dynamics

- Climate change

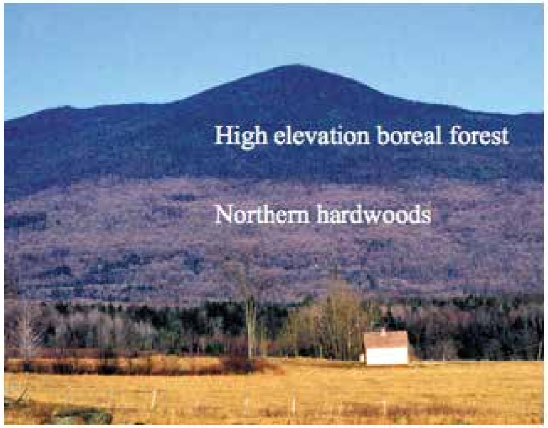
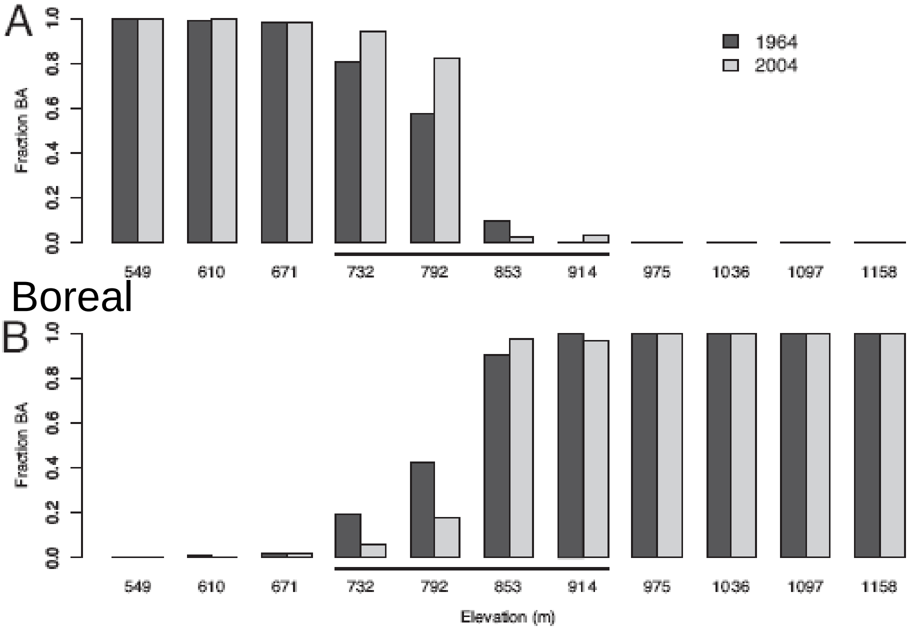


Fig. 1. The distinct zonation of northern hardwood and boreal forests with elevation on Mount Abraham in the Green Mountains of Vermont. [Reproduced with permission from ref. 39 (Copyright 2003, American Meteorological Society).]

Hardwood

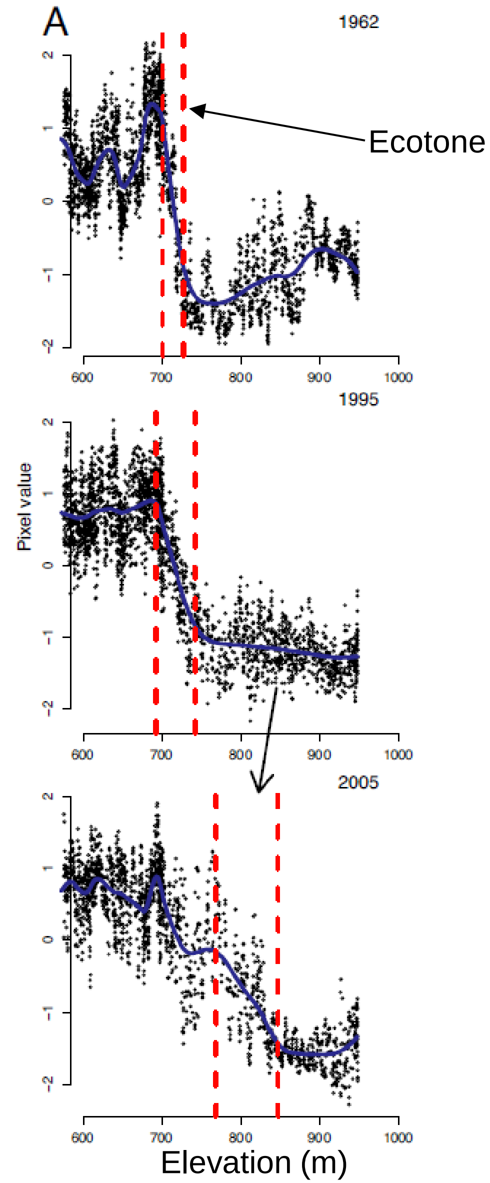
Boreal



Beckage et al. 2008

Temporal and spatial dynamics

- Climate change
  - ~90-120 m upward shift in ecotone in 40 yrs
  - Only a 1.1°C temp. increase (& ~34% precip. Increase)
  - Given larger expected changes in temp. & precip., where will the boreal forest go?



Beckage et al. 2008

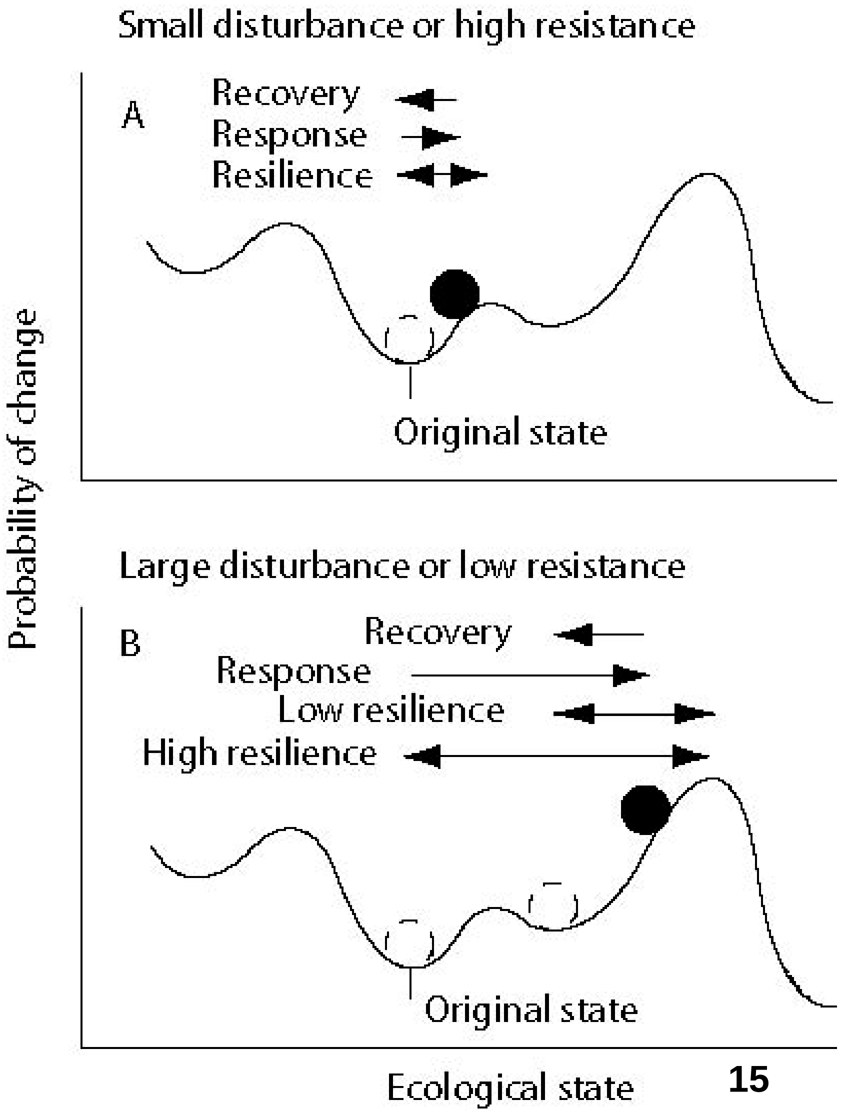
Temporal and spatial dynamics

- Disturbances
  - *A relatively discrete event in time that disrupts ecosystem structure, and changes resource availability and the physical environment*
  - Integral part of ecosystem functioning
    - One of the interactive controls on ecosystem processes
  - Disturbance results in ecological succession
    - *Directional change in species composition, structure, & resource availability over time that is driven by biotic activity & interactions, & changes in the physical env.*
  - Disturbance properties are important
    - Type, severity, intensity, frequency, size, timing, etc.

Temporal and spatial dynamics

Ecosystem response to disturbance depends on

- Resistance: Tendency to not change
- Response: Magnitude of change
- Resilience: Capacity to return to previous state
- Recovery: Extent of return to previous state

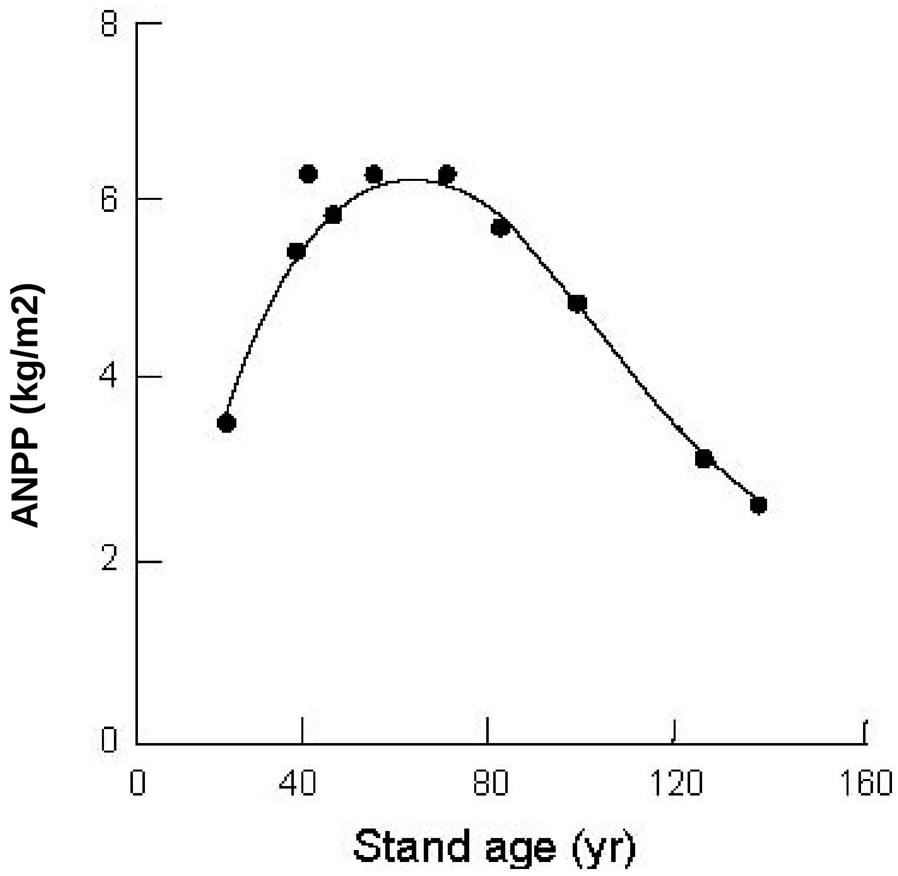


Temporal and spatial dynamics

- Disturbances → Ecological Succession
  - Leads to temporal and spatial variability within and across ecosystems
    - Patchiness across the landscape
  - In the absence of further disturbance, may lead to a “climax” community or “steady state”
    - Early colonizers give way to late successional species
  - Multiple pathways of succession are possible, depending on distance to seed source, severity/intensity of disturbance, etc.
    - Alternative steady (or stable) states

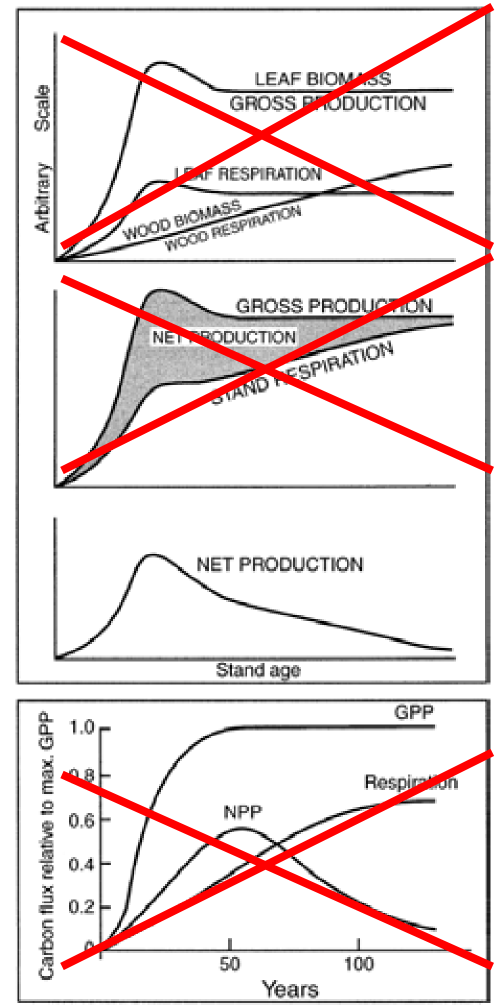
Temporal and spatial dynamics

- Forest ANPP typically highest at mid-succession
- Declines strongly following canopy closure
- Why?



Temporal and spatial dynamics

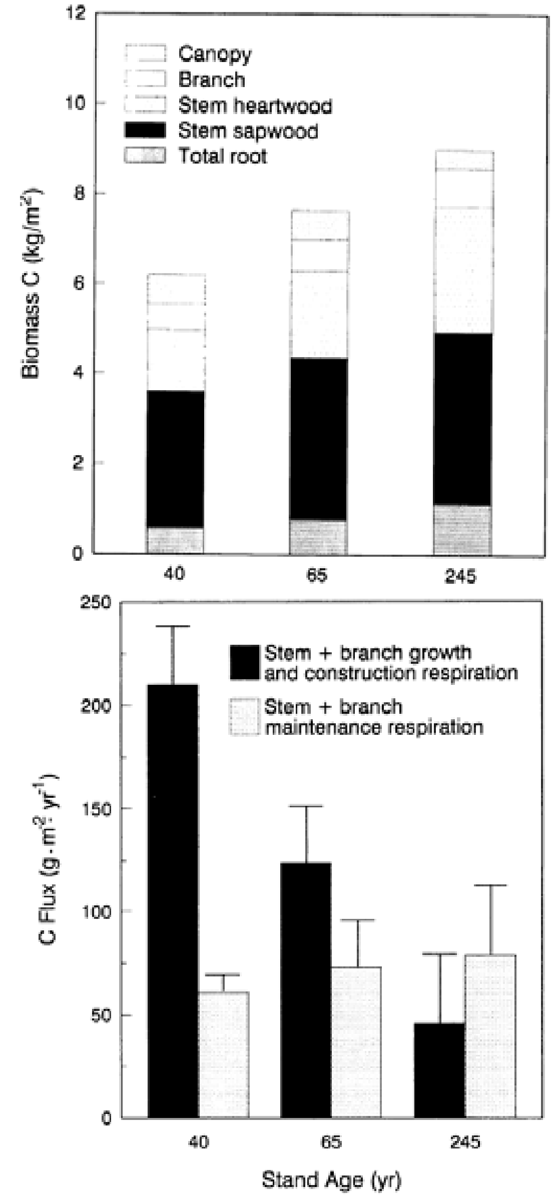
- Why does NPP decline w/ stand age?
  - Peak in GPP & NPP with canopy closure
  - Slight decline in GPP as leaf area ↓, but more or less constant after canopy closure
  - NPP declines sharply following canopy closure
  - $R_{foliage}$ peaks & constant after canopy closure
  - Respiration model (intuitive and easy)
    - Wood respiration continues to increase as woody biomass accumulates
    - Widely accepted, and in <u>every</u> textbook
      - Despite the fact that the only existing study did not support it
      - So widely accepted, that the transient decrease in GPP is largely ignored, and the increase in wood respiration is used as the one and only causal mechanism



Ryan et al. (2004)

Temporal and spatial dynamics

- Ryan & Waring (1992) quantified R_{growth} and R_{maint} across an age sequence of *P. contorta*
- Wood biomass increased with age
- R_{growth} declined with age
- Slight increase in R_{maint} with age could <u>not</u> explain decrease in NPP with stand age



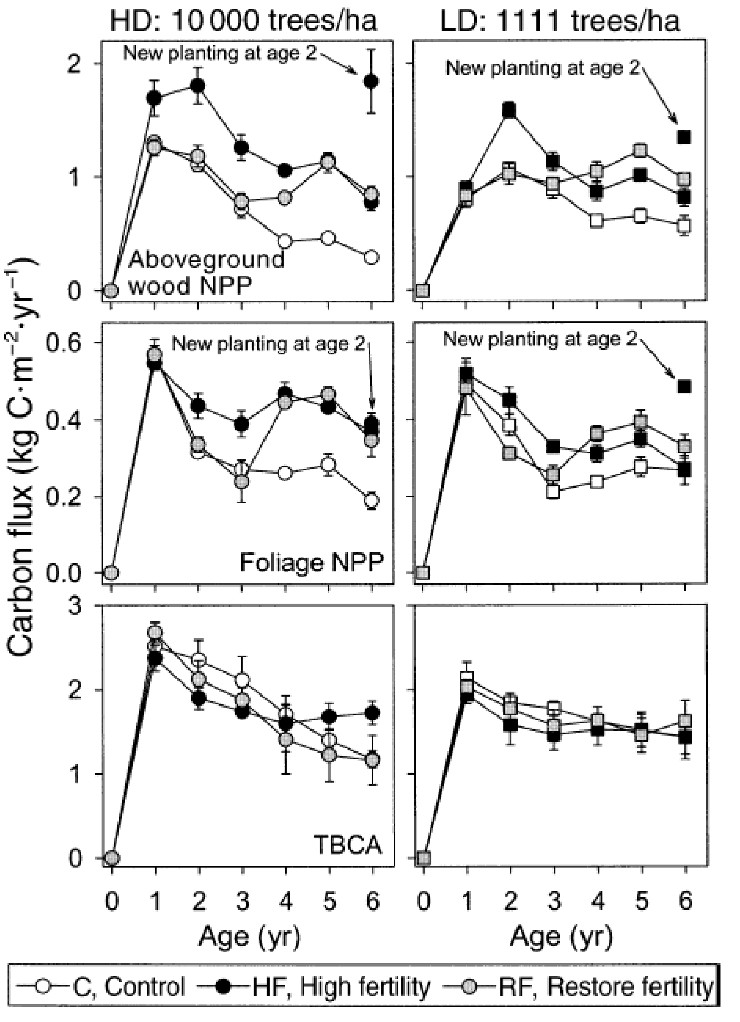
Ryan & Waring (1992)

Temporal and spatial dynamics

- Then what does explain declining NPP_{wood} as stands age? (Ryan et al. 2004)
  - H1: GPP does not decline, but NPP declines because:
    - Higher partitioning to wood respiration and/or
    - Higher partitioning to belowground
  - H2: GPP declines with stand age and the decline in NPP is proportional to the decline in GPP
    - Reduced LAI and photosynthesis as nutrients become limiting
    - Abrasion between tree canopies
    - Hydraulic limitations as tree height increases
  - H3: GPP declines, but decline in NPP is disproportionately larger because C allocation also changes

Temporal and spatial dynamics

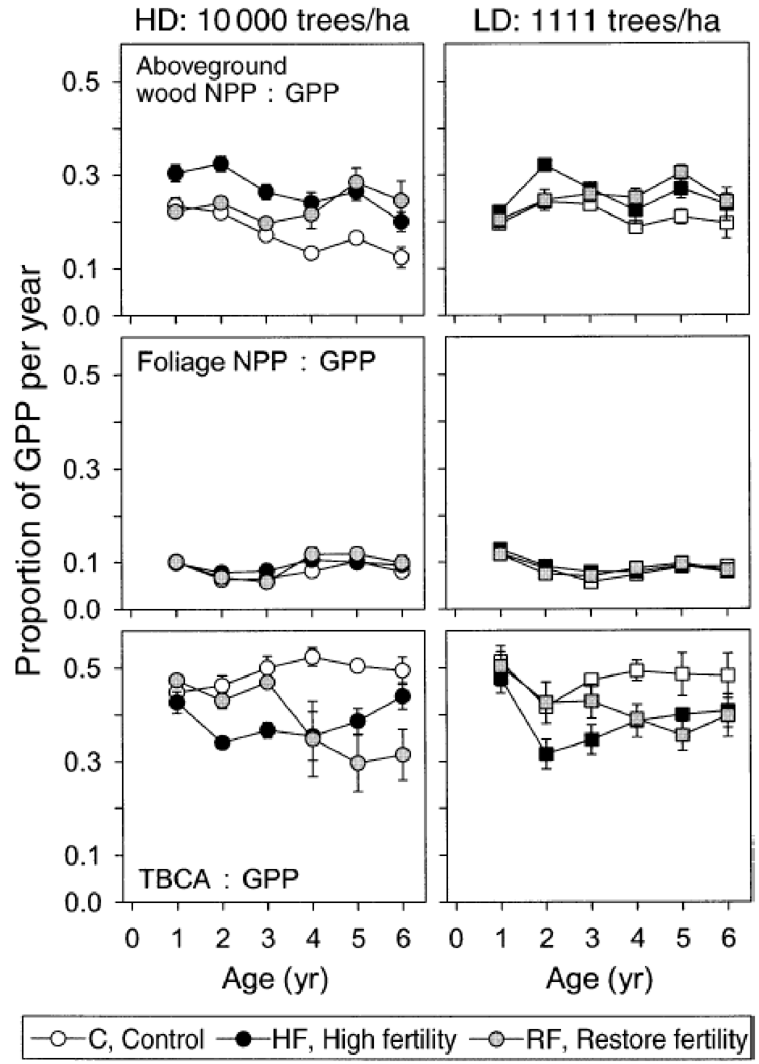
- GPP declined (H1 failed)
  - Not caused by nutrient limitation, a decline in leaf area or in photosynthetic capacity, or by hydraulic limitation.
- GPP declined, but the decline in NPP was proportionately larger (H2 failed)



Ryan et al. (2004)

Temporal and spatial dynamics

- Data supports H3
  - GPP declined and the decline in NPP was accompanied by a shift in partitioning (belowground partitioning increased with age)



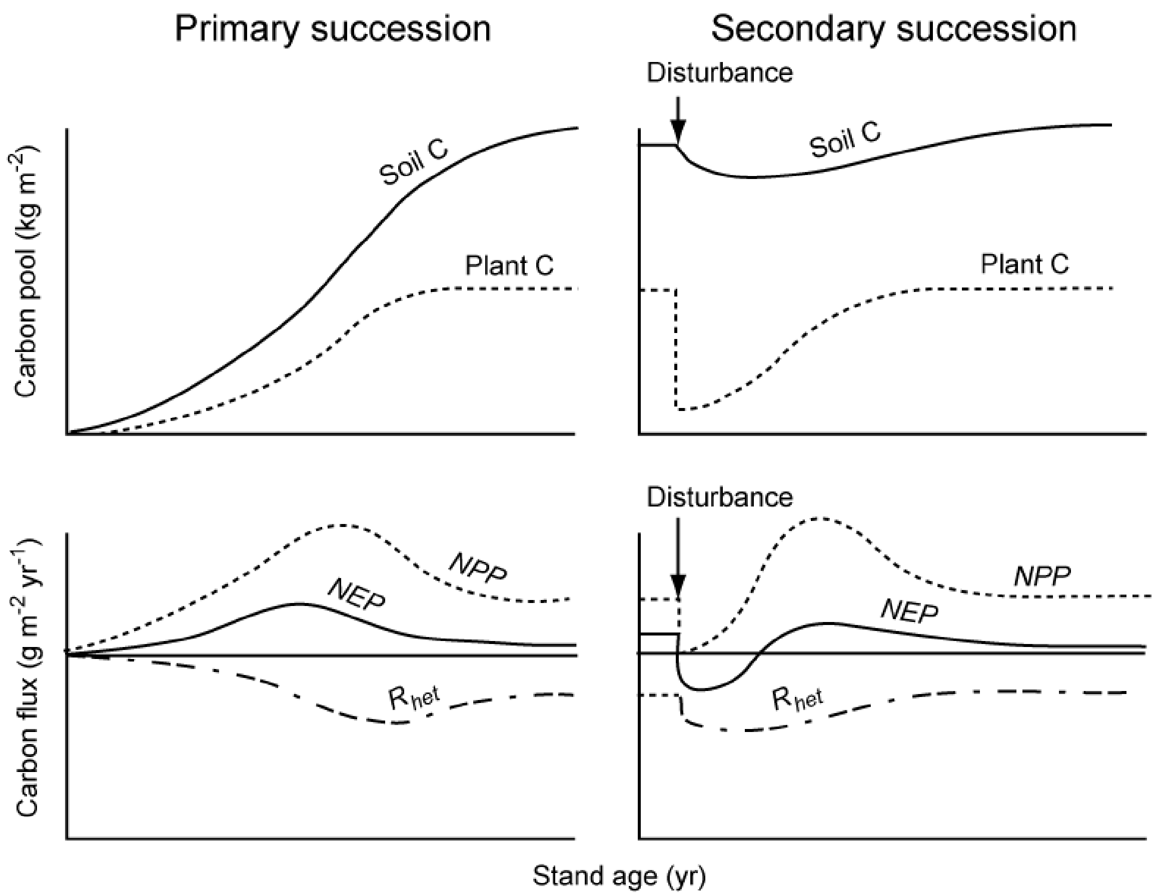
Ryan et al. (2004)

Temporal and spatial dynamics

- *Why does GPP decline with stand age when LAI and photosynthetic capacity remain high?*
  - Ryan et al. (current)
    - *Eucalyptus* plantations in Brazil
    - Changes in growth result from changes in dominance & the efficiency of resource use by dominant vs. non-dominant trees
  - Drake et al. (2011)
    - *Pinus* plantations in N.C.
    - Reduced stomatal conductance and photosynthesis w/ age
      - » R_{wood} declined with stand age
      - » Hydraulic limitation decreased GPP & NPP
  - Still a lot of debate, with important implications

Temporal and spatial dynamics

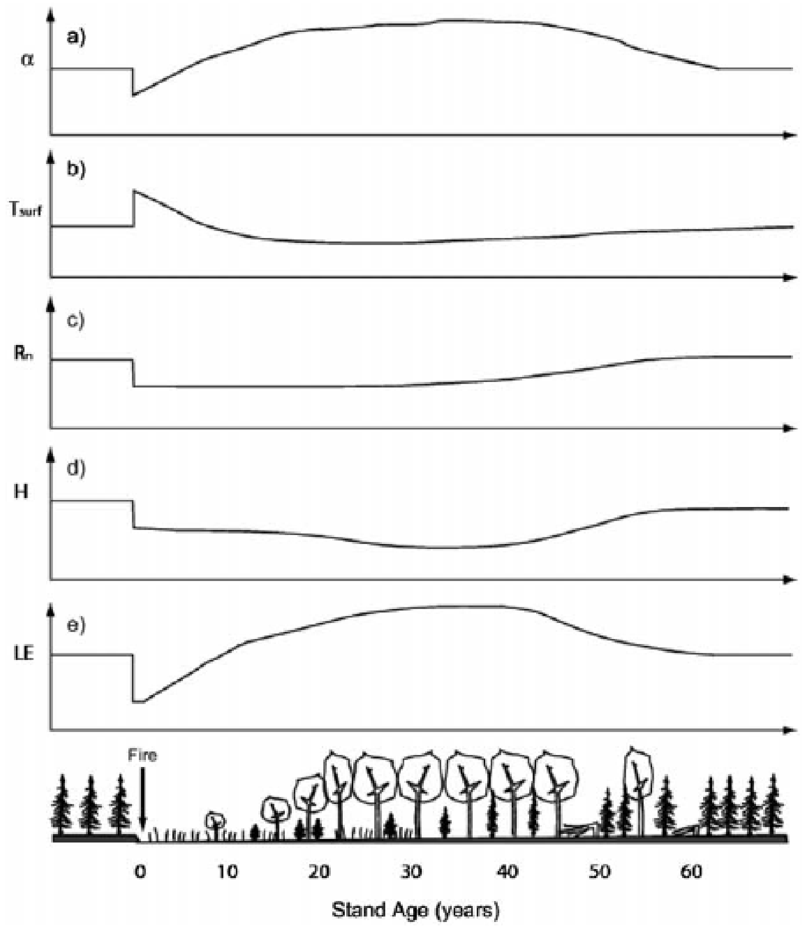
- How do C pools & fluxes change with stand age across a landscape following disturbance?



Kashian et al. 2006

Temporal and spatial dynamics

- Energy balance changes after disturbance and thru succession



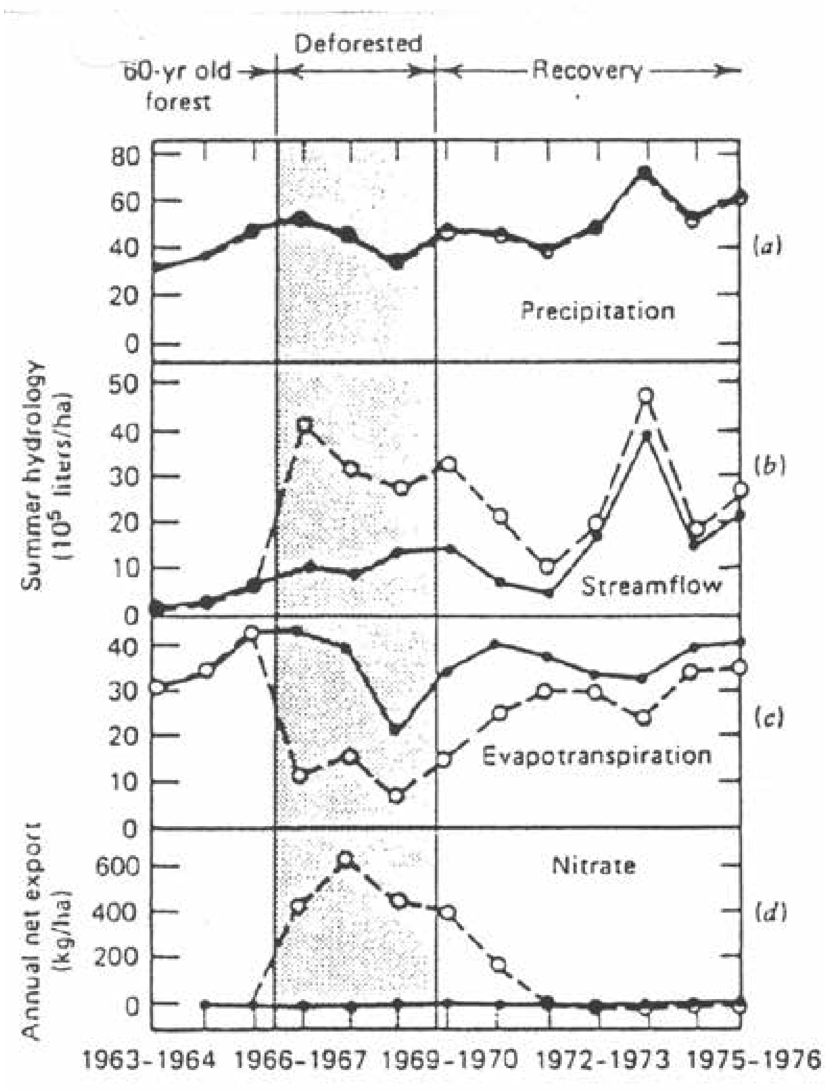
Liu & Randerson 2007

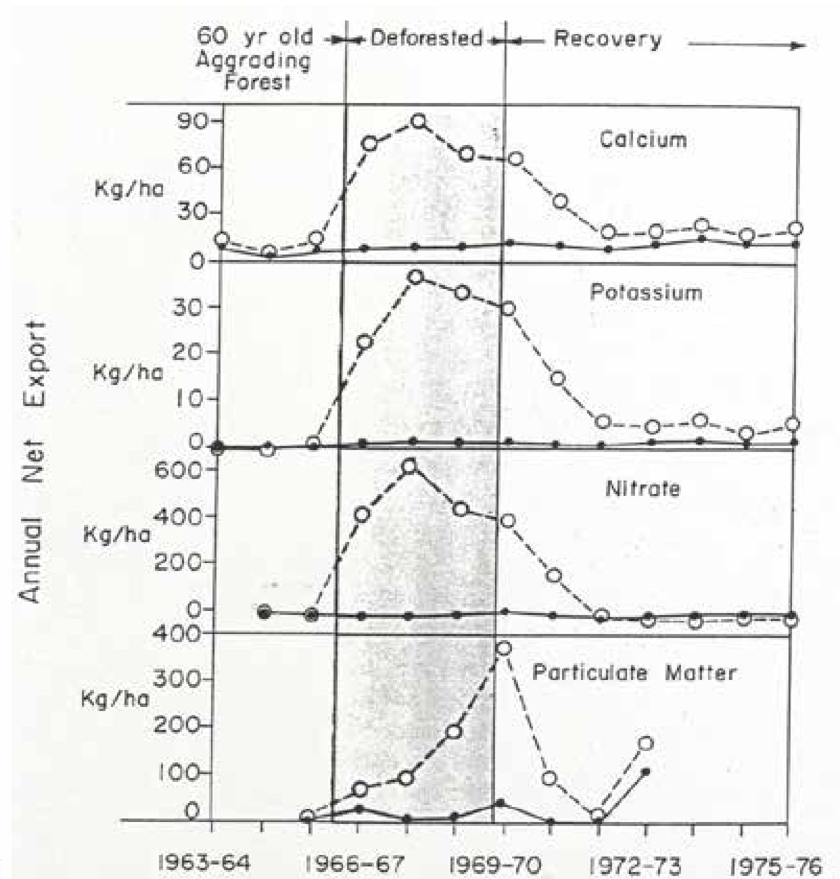
Temporal and spatial dynamics

- Nutrient cycling changes after disturbance & thru succession
  - Pulse of nutrient availability after disturbance
    - Fate depends on retention mechanisms
      - Plant uptake
      - Microbial uptake
      - Chemical fixation
  - Changes in nutrient availability are variable
    - May remain high for some time (e.g., temperate forests)
    - May decline rapidly (e.g., boreal forests)

Hubbard Brook Watershed Studies

(Likens, G. E., F. H. Bormann, R. S. Pierce and W. A. Reiners. 1978. Recovery of a deforested ecosystem. Science 199(4328):492-496)





Temporal and spatial dynamics

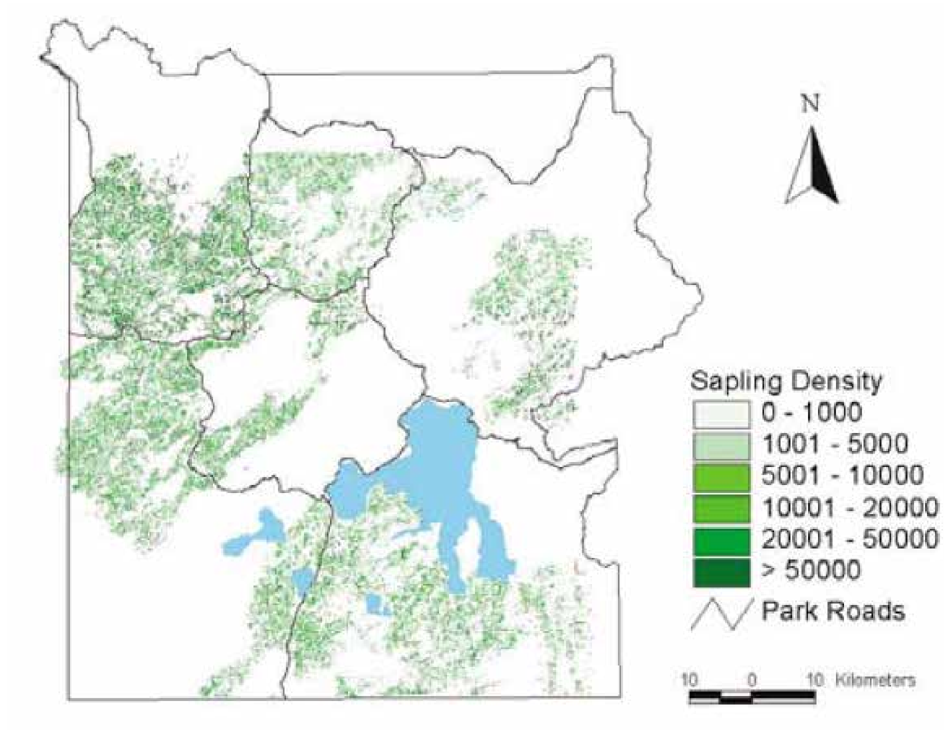
- Spatial heterogeneity
  - Critical to the functioning of both individual ecosystems and entire regions
  - Plays out largely via exchange of energy & materials
    - Across ecosystem types
    - Within ecosystem types
  - Landscapes are mosaics of patches
    - Differ in ecologically important properties
  - Size, shape, connectivity, and configuration of patches on a landscape influence interactions
    - Interact via movement of energy (C), water, air, materials, organisms, disturbances, etc.

Temporal and spatial dynamics

- Fires → spatial heterogeneity
  - Turner et al. (2004) asked how this influences spatial variability in important ecosystem properties
  - How do differences in postfire stand density across the landscape influence LAI & ANPP?
    - Postfire stand density explained by fire severity, distance to nearest unburned edge, pre-fire species composition, and % serotiny in stand

Temporal and spatial dynamics

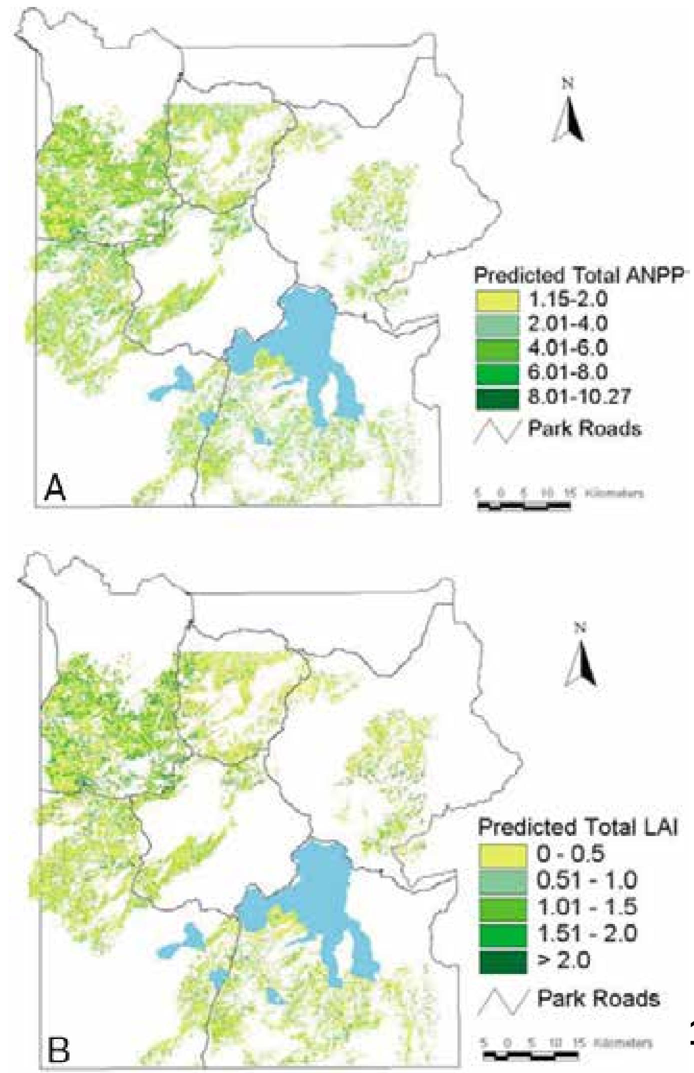
- Very large spatial variability in postfire regeneration



Turner et al. 2004

Temporal and spatial dynamics

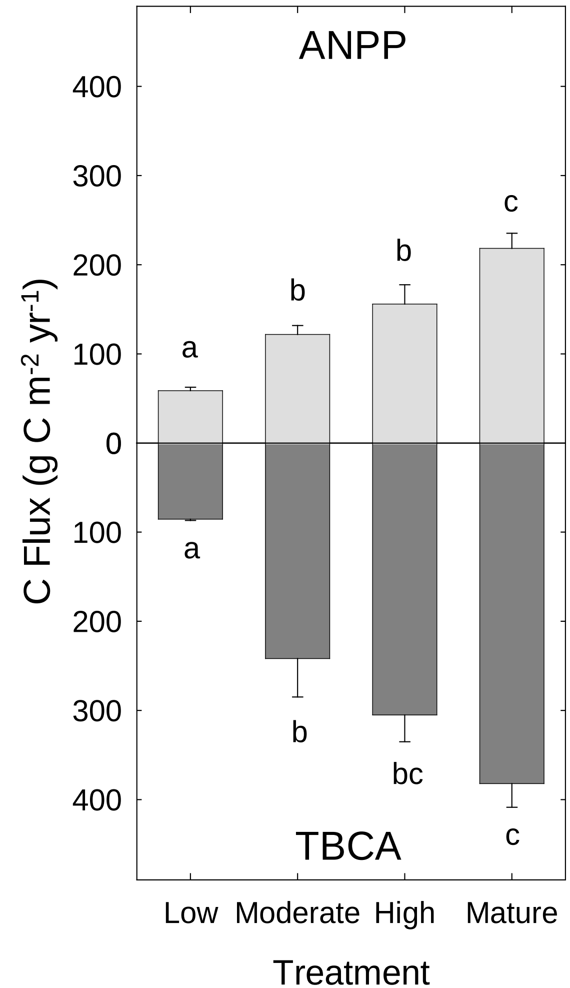
- Led to large spatial heterogeneity in ecosystem structure (LAI) and function (ANPP)
- Spatial heterogeneity within a single successional stage was similar in magnitude to that observed throughput succession (over stand development)!!!



Turner et al. 2004

Temporal and spatial dynamics

- Litton et al. (2004) expanded upon this work
  - Built complete C budgets (above- and belowground)
  - How does spatial variability in postfire stand density and age influence C dynamics?



Litton et al. 2004