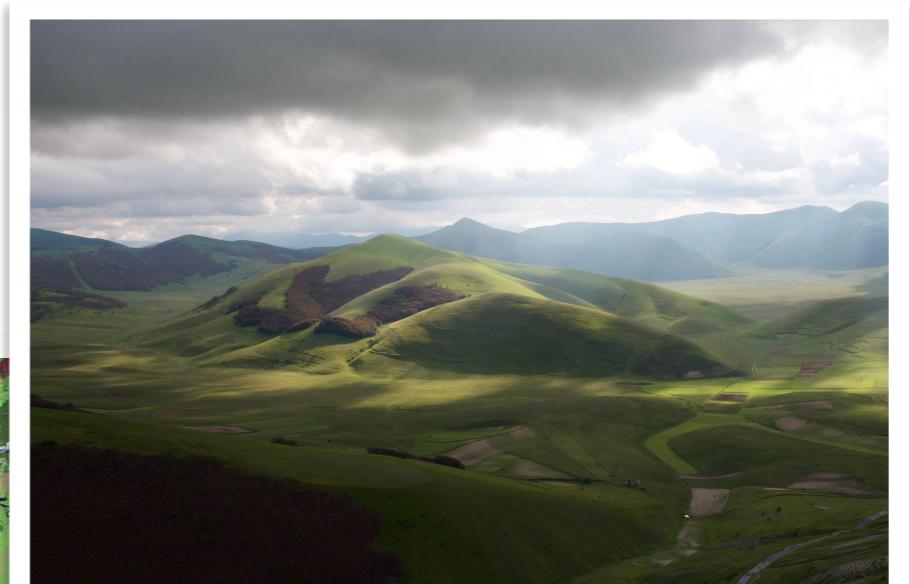
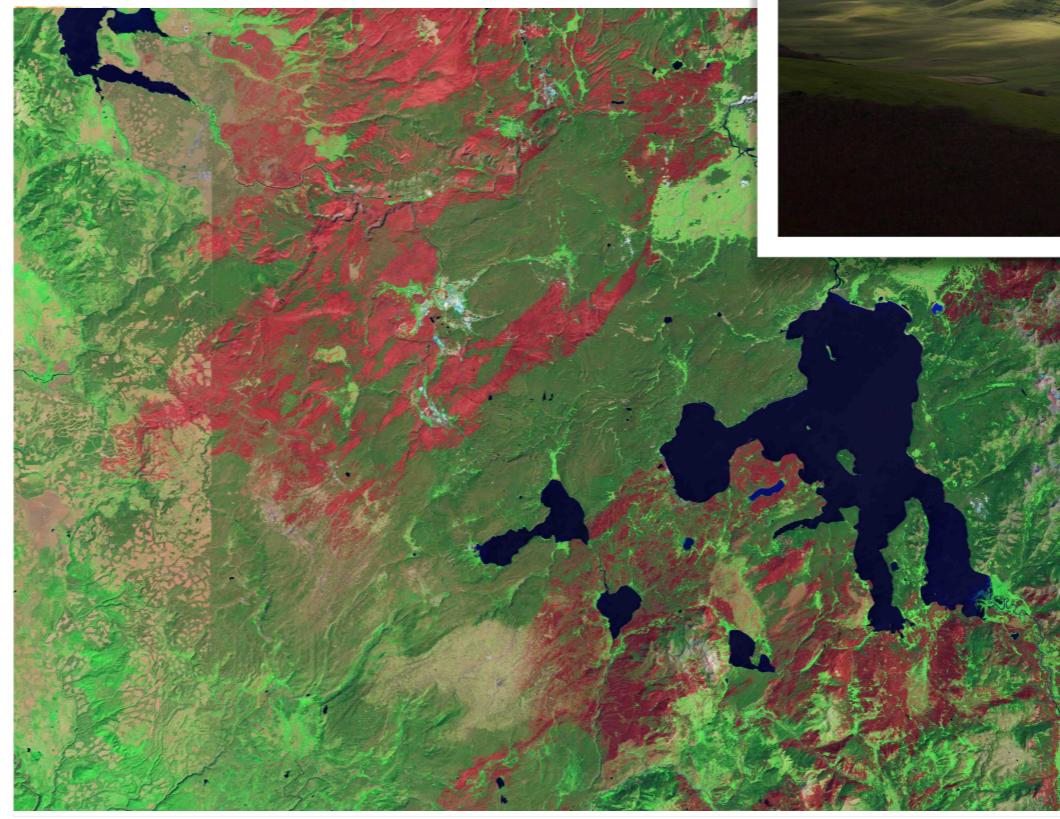
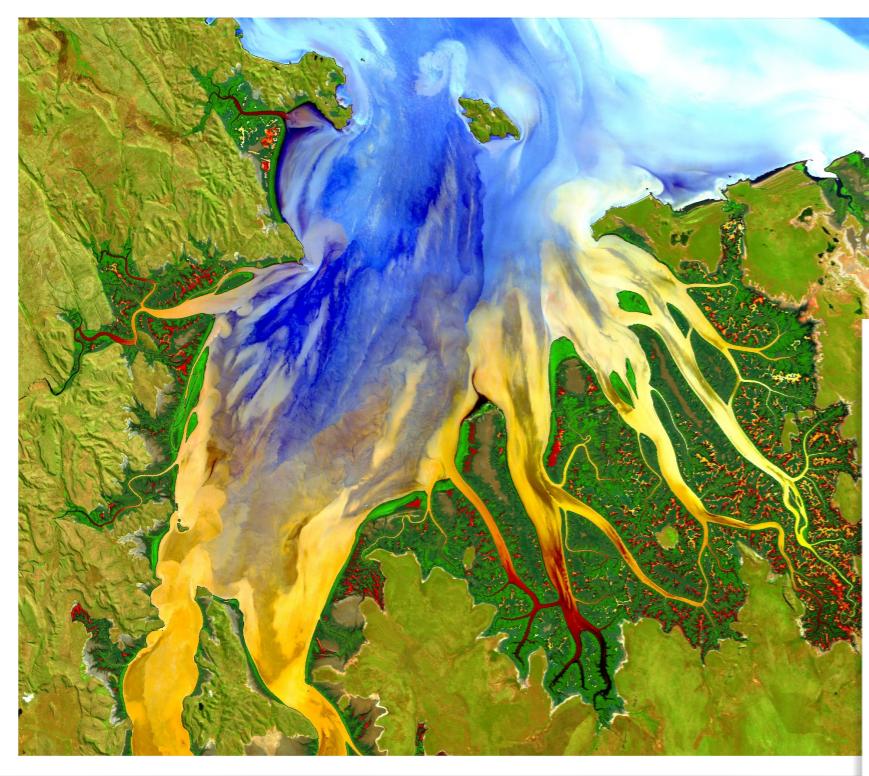
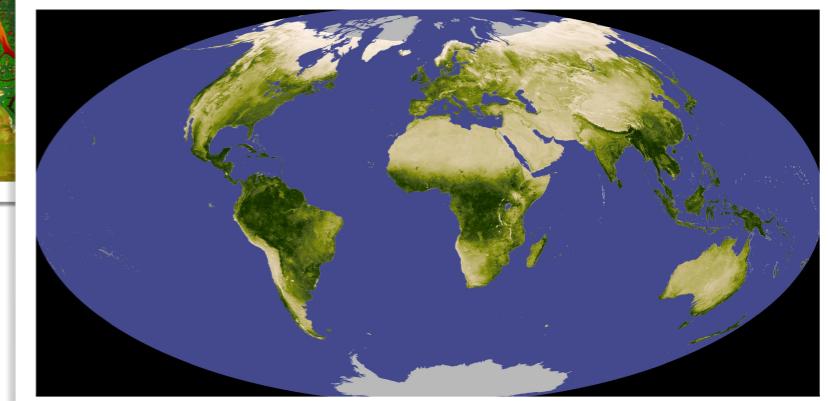
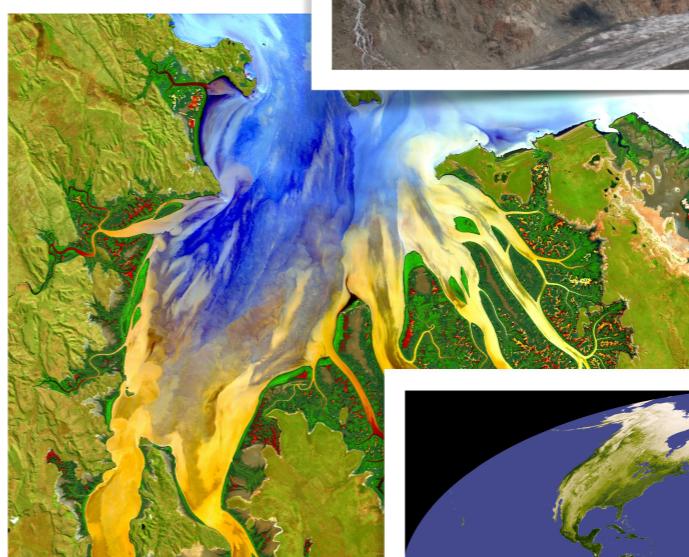
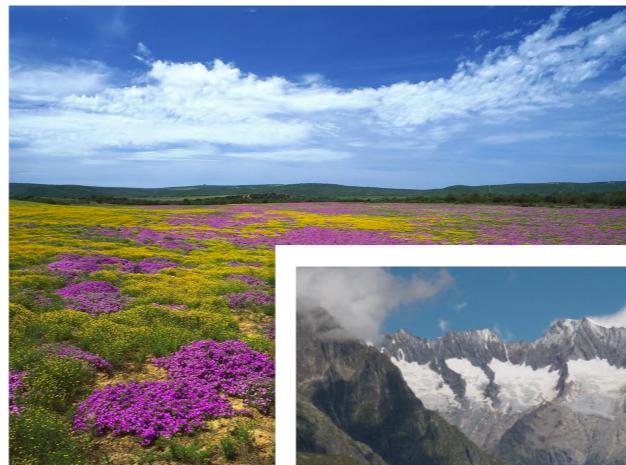


Agents of Spatial Pattern



Learning objectives

- Define the primary drivers of spatial patterns in terrestrial ecosystems (focus on vegetation)
- Describe how these drivers interact and how their influence changes across scales
- Explain the role / interplay of history and spatial patterns (Foster (1992) discussion)

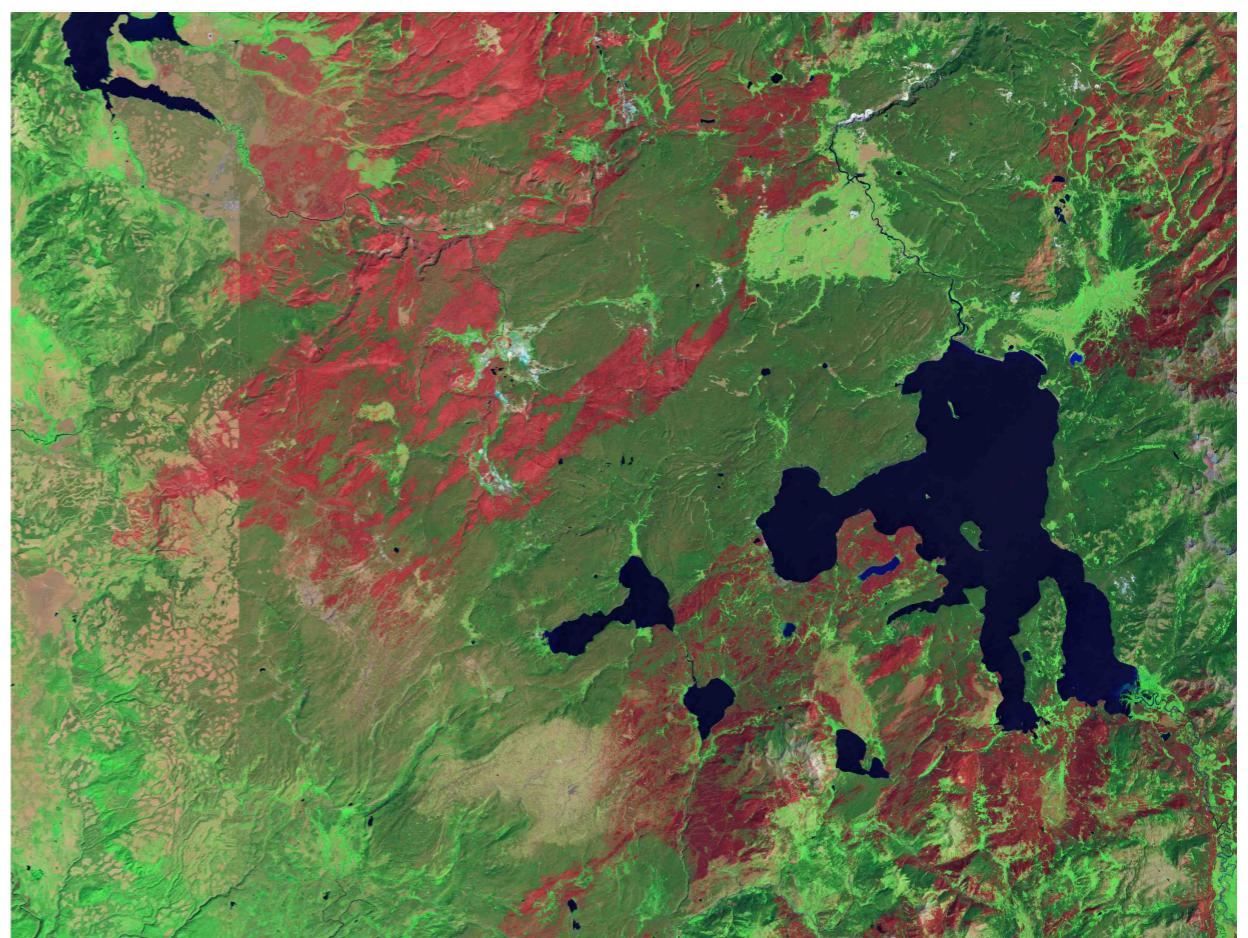


Spatial ecology is the study of the interplay between spatial patterns and ecological processes.

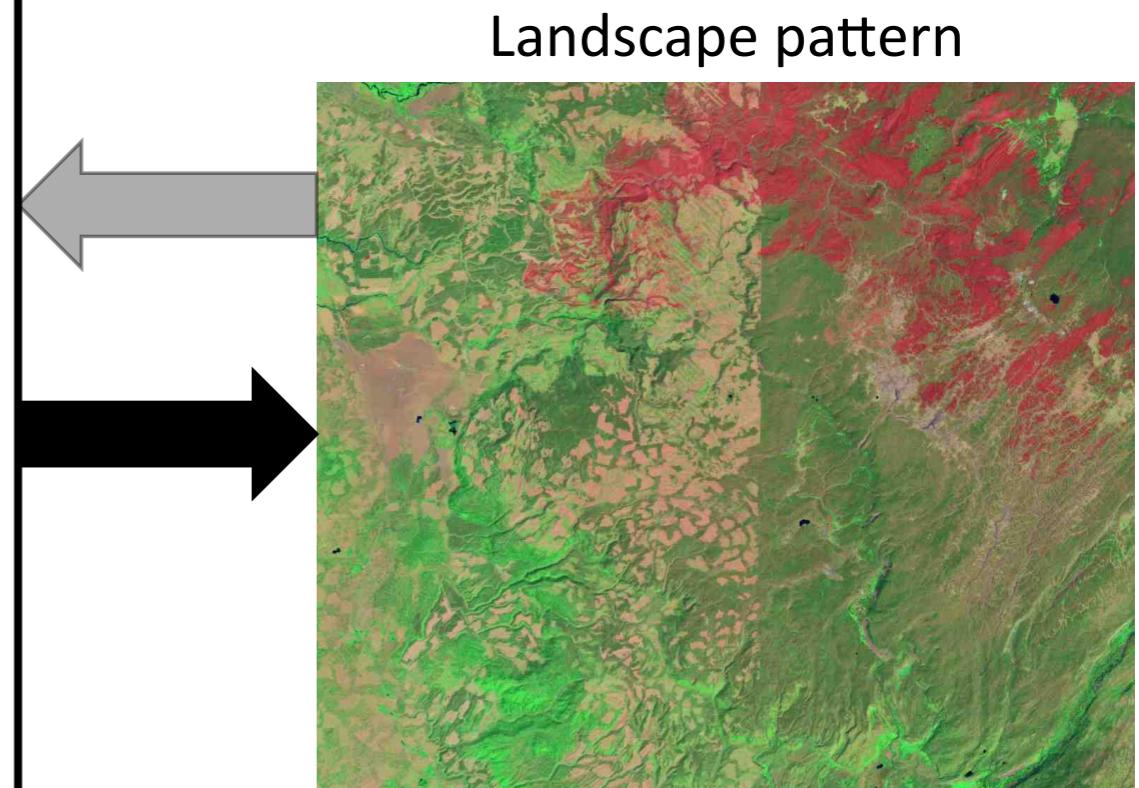
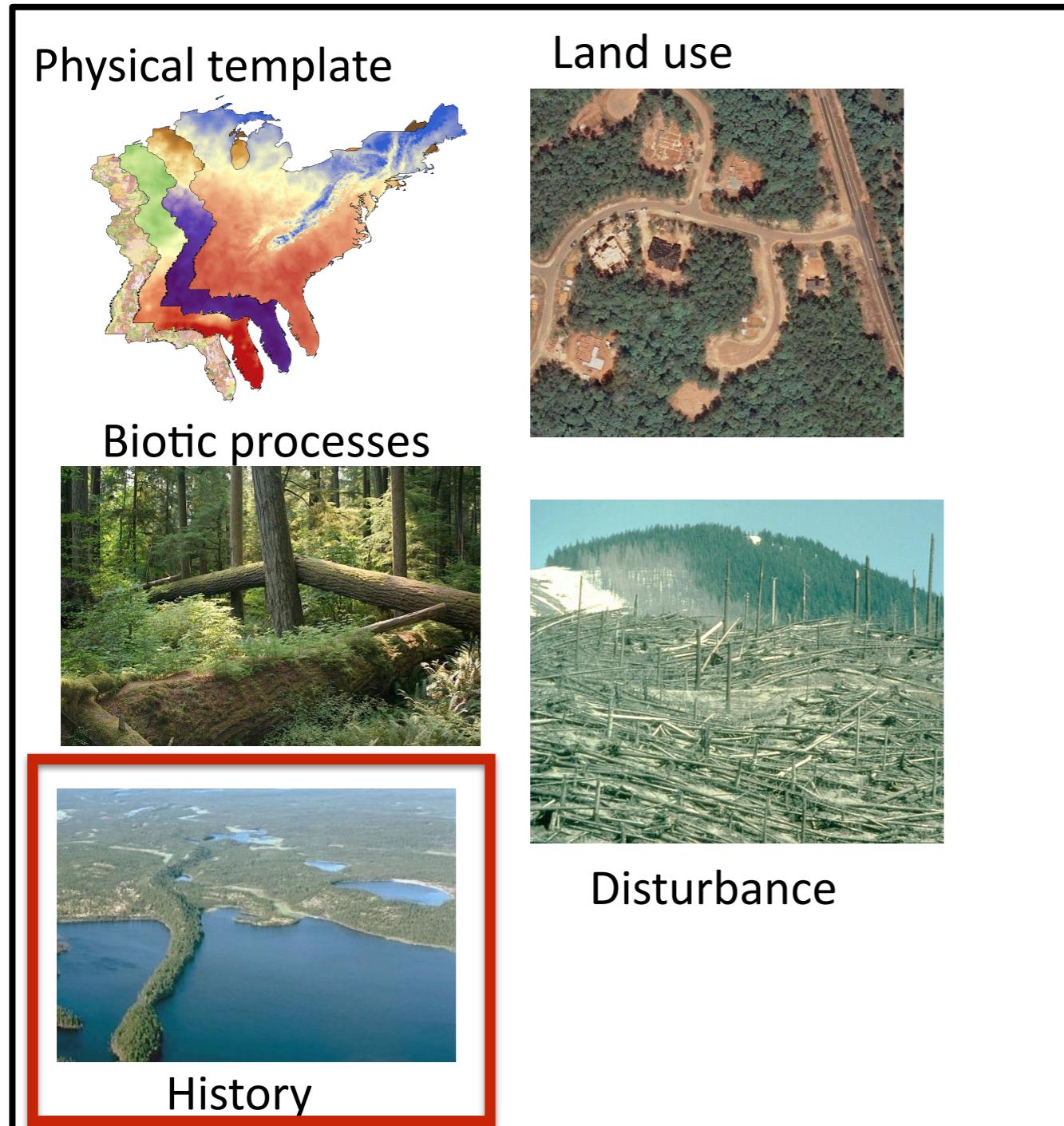
So what are the primary causes of spatial patterns & at what scales do these factors operate?

Four (or so) primary drivers

1. **Abiotic conditions** (physical template) - climate, topography / landform, soils, flow, depth/ light, salinity, temperature, nutrients, turbidity
2. **Biotic processes** - interactions between species, demographic processes - including dispersal
3. **Disturbance** and succession
4. **Land use** (past and present)
5. **History**



Primary Drivers



constant interplay between the primary drivers and the landscape.

Unit and scale of study of patterns

- Vegetation bias: focus on patterns of dominant vegetation (easily identified and studied)
 - Patterns in fauna and other ecosystem components typically track vegetation
 - Two scales are common
 - Continental (biomes / life zones)
 - Landscape (ecotones)

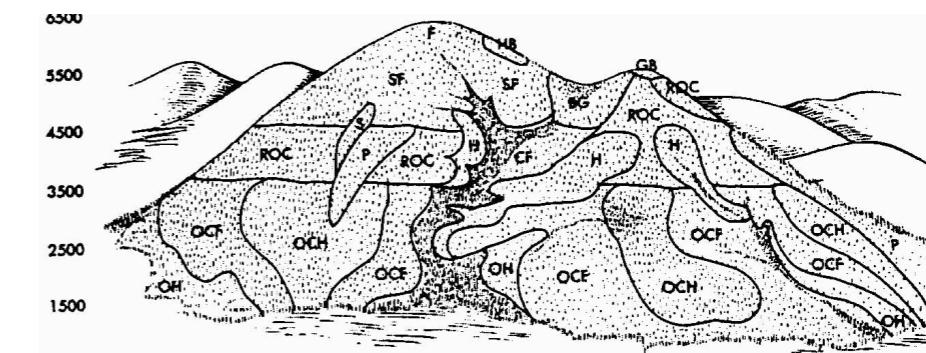


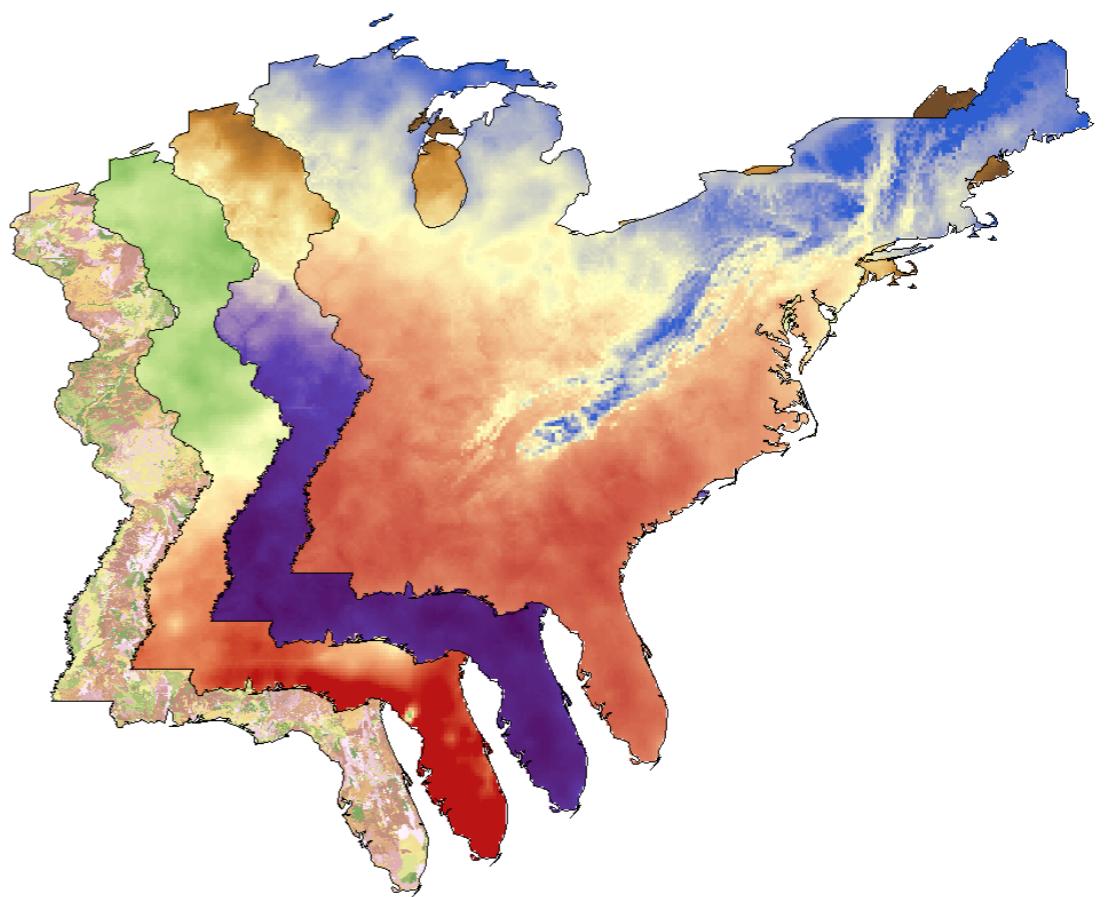
Figure 10.9. Topographic distribution of vegetation types on an idealized west-facing mountain and valley in the Great Smoky Mountains. Vegetation types: BG, beech gap; CF, cove forest (darker shading indicates steep slopes); F, Fraser fir forest; GB, grassy bald; H, hemlock forest; HB, heath bald; OCF, chestnut oak—chestnut forest; OCH, chestnut oak—chestnut

figure on gradient analysis depicting differing forest types within a small mountain area

The Physical (abiotic) Template

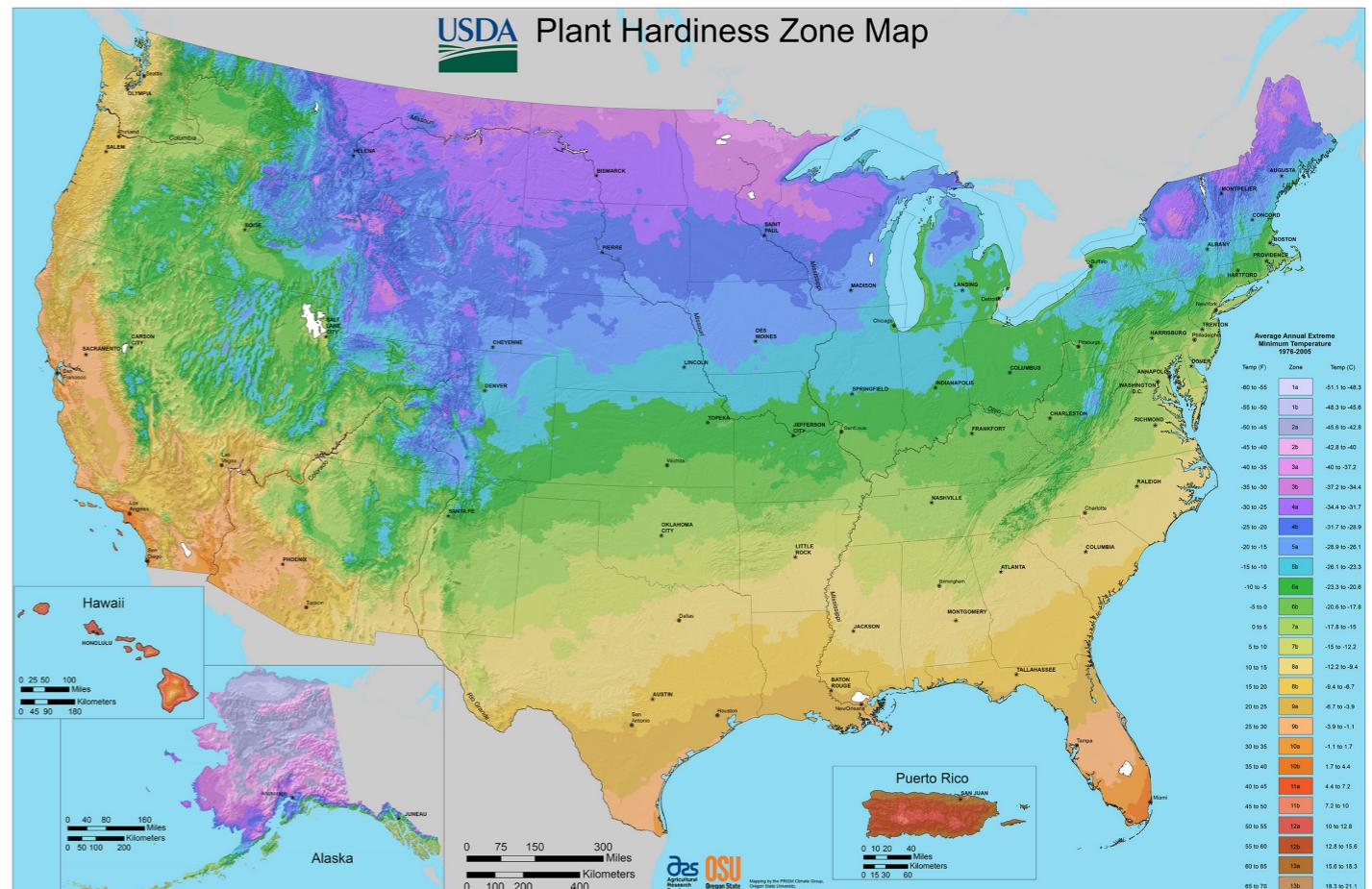
Three primary physical / abiotic drivers of spatial pattern

1. Climate
2. Landform
3. Soils



The Physical (abiotic) Template

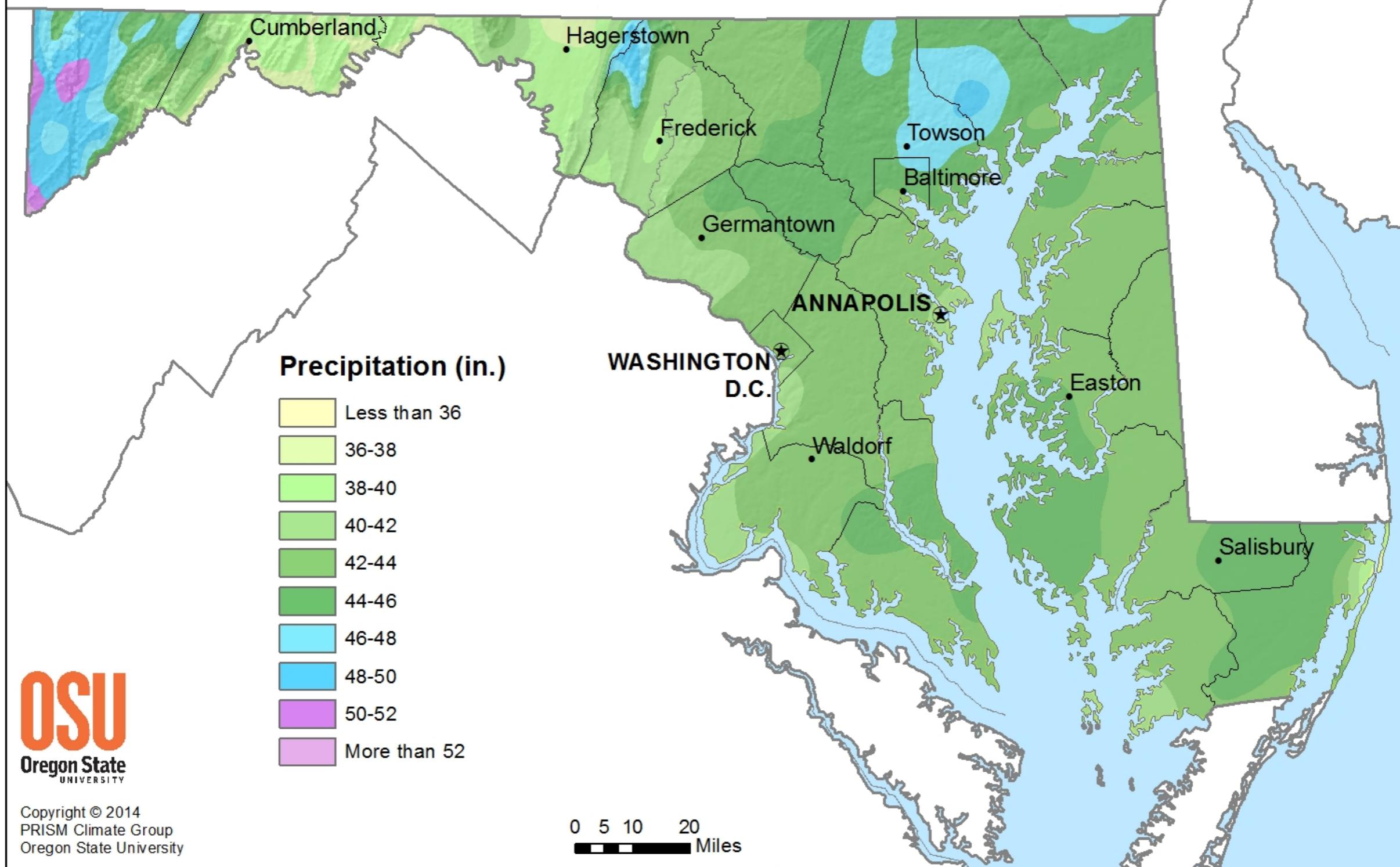
- **Climate:** long-term (30-year average), generally prevailing weather (but extreme events very important)
 - acts as strong control on biogeographical patterns through the distribution of energy and water
 - Latitudinal & elevational gradients
 - climate change will (and has) profoundly alter landscape patterns & processes



based on the probability of expected minimum winter temperatures by zone.

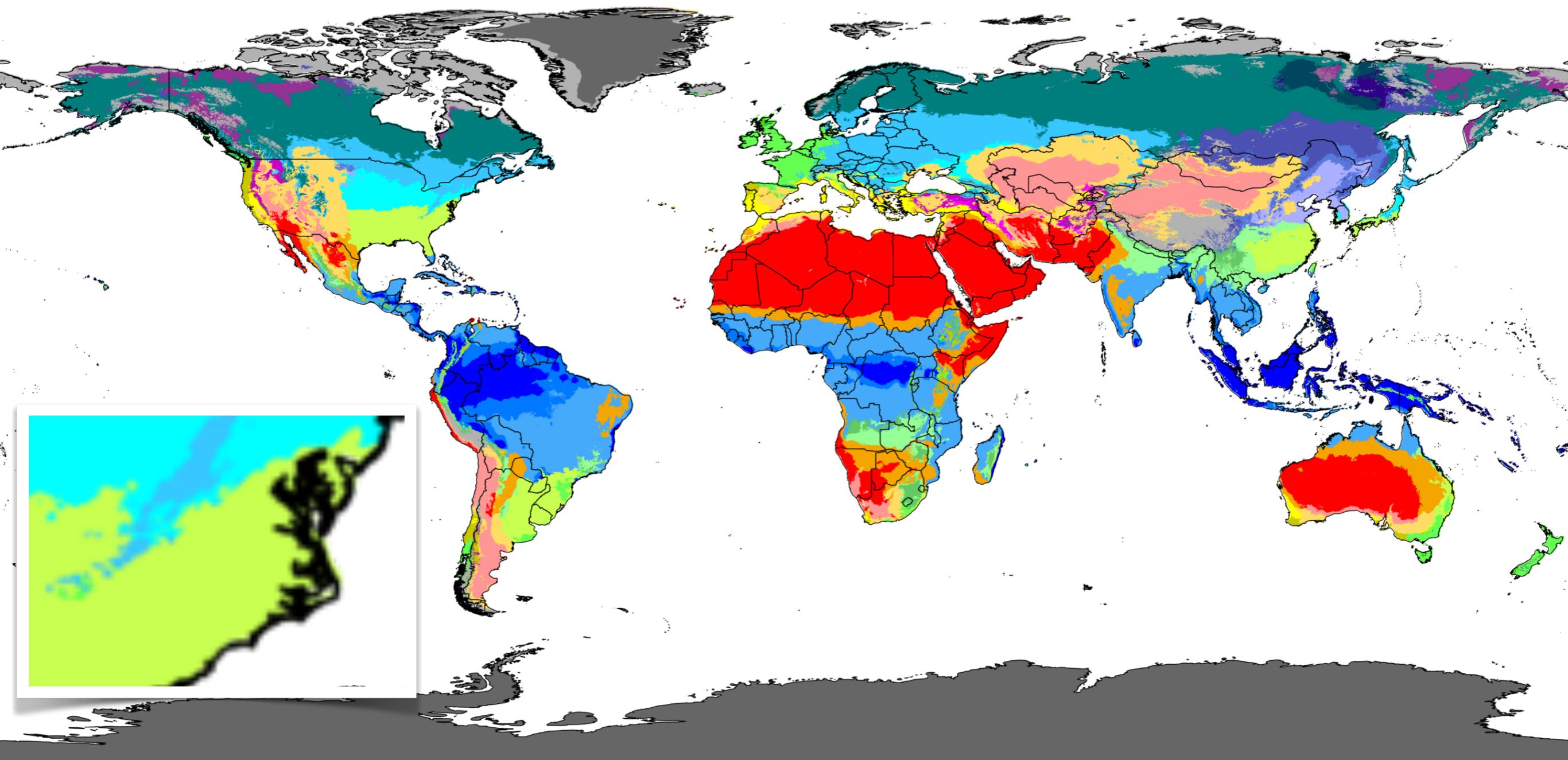
Average Annual Precipitation (1981-2010)

Maryland & District of Columbia



Copyright © 2014
PRISM Climate Group
Oregon State University

Köppen-Geiger climate classification map (1980-2016)



Source: Beck et al.: Present and future Köppen-Geiger climate classification maps at 1-km resolution, Scientific Data 5:180214, doi:10.1038/sdata.2018.214 (2018)

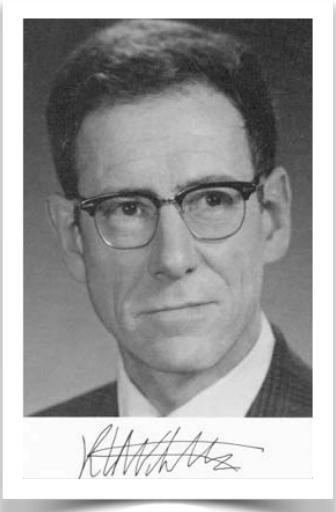
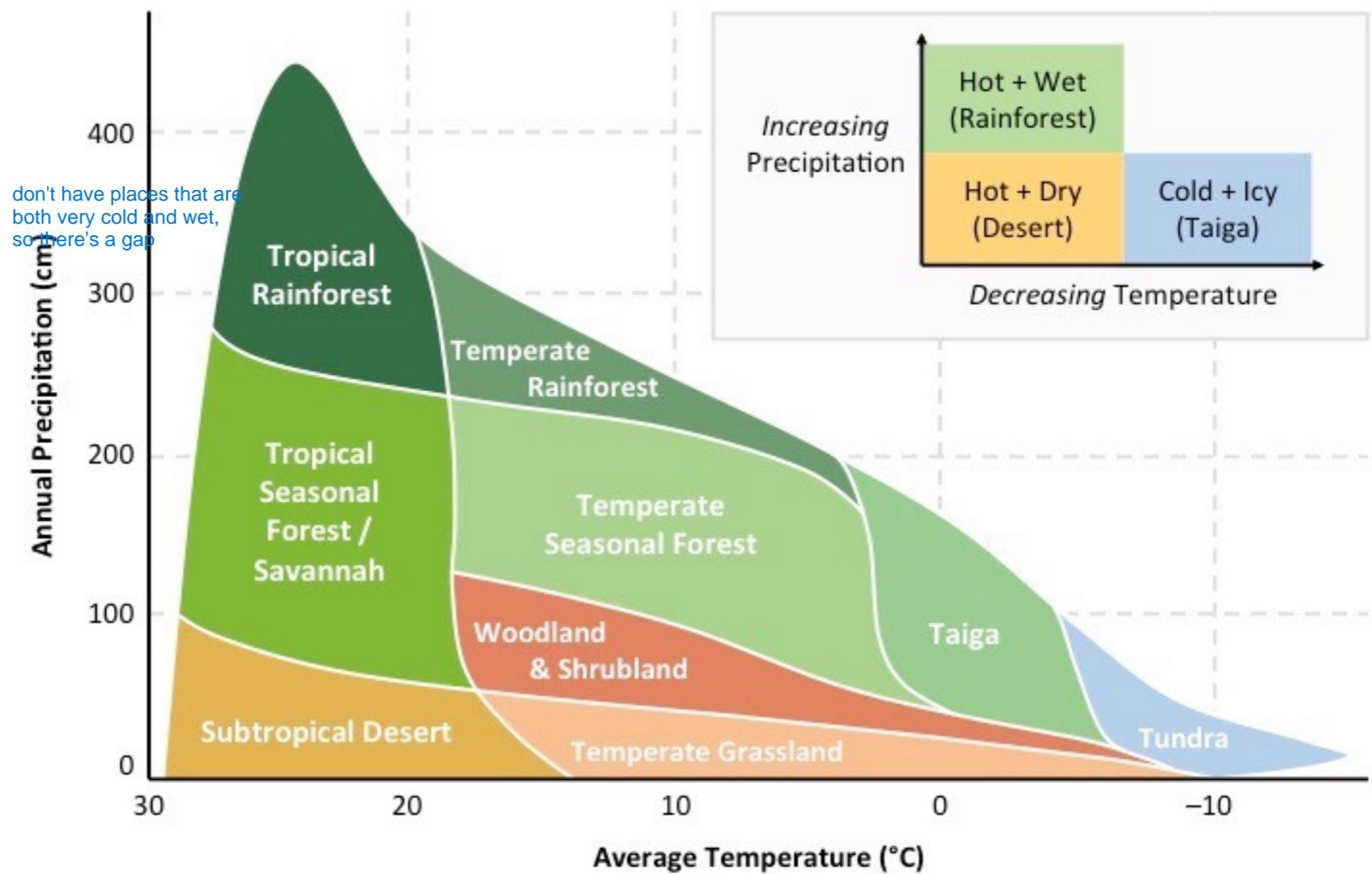
College Park = Humid subtropical climate

Maryland spans three climate zones.

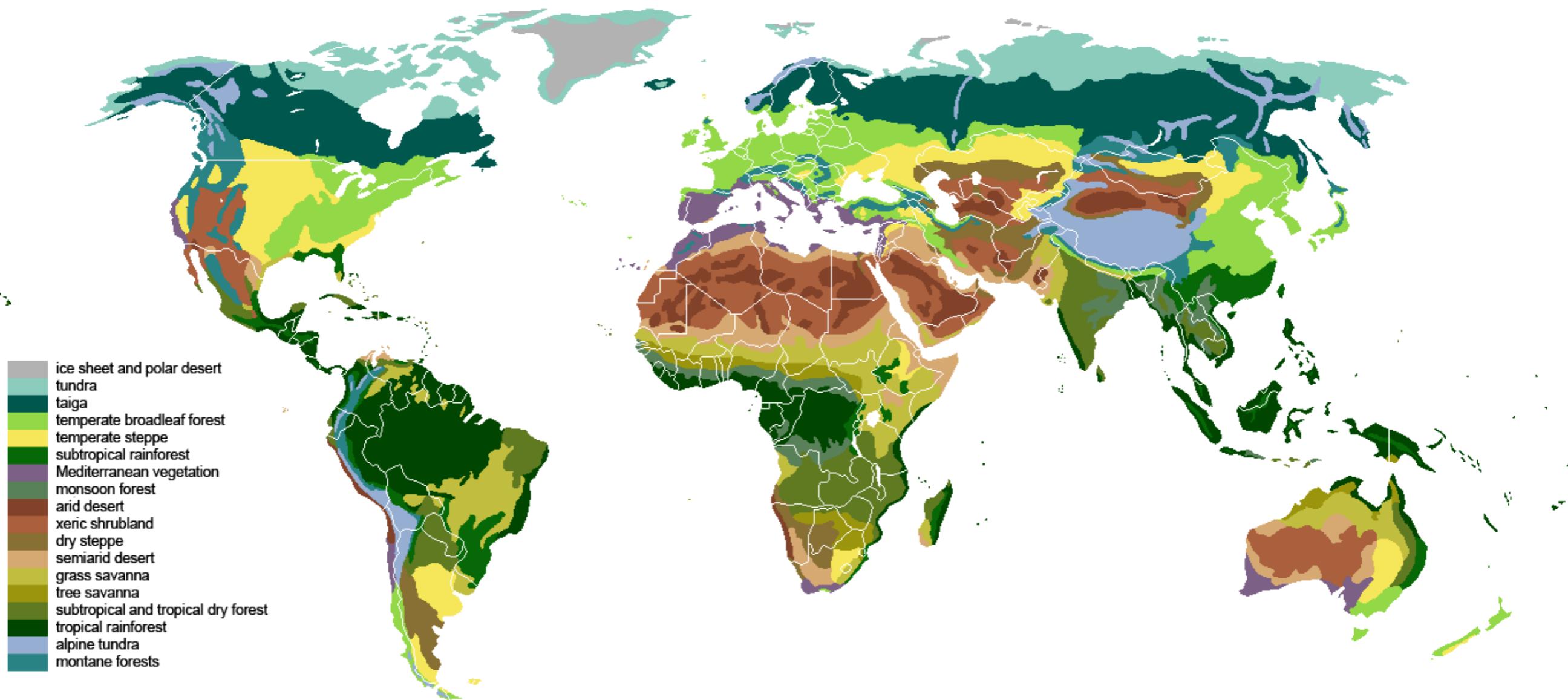
Cumberland = Hot summer continental climate

Frostburg = Warm summer continental climate

Whittaker's Climograph



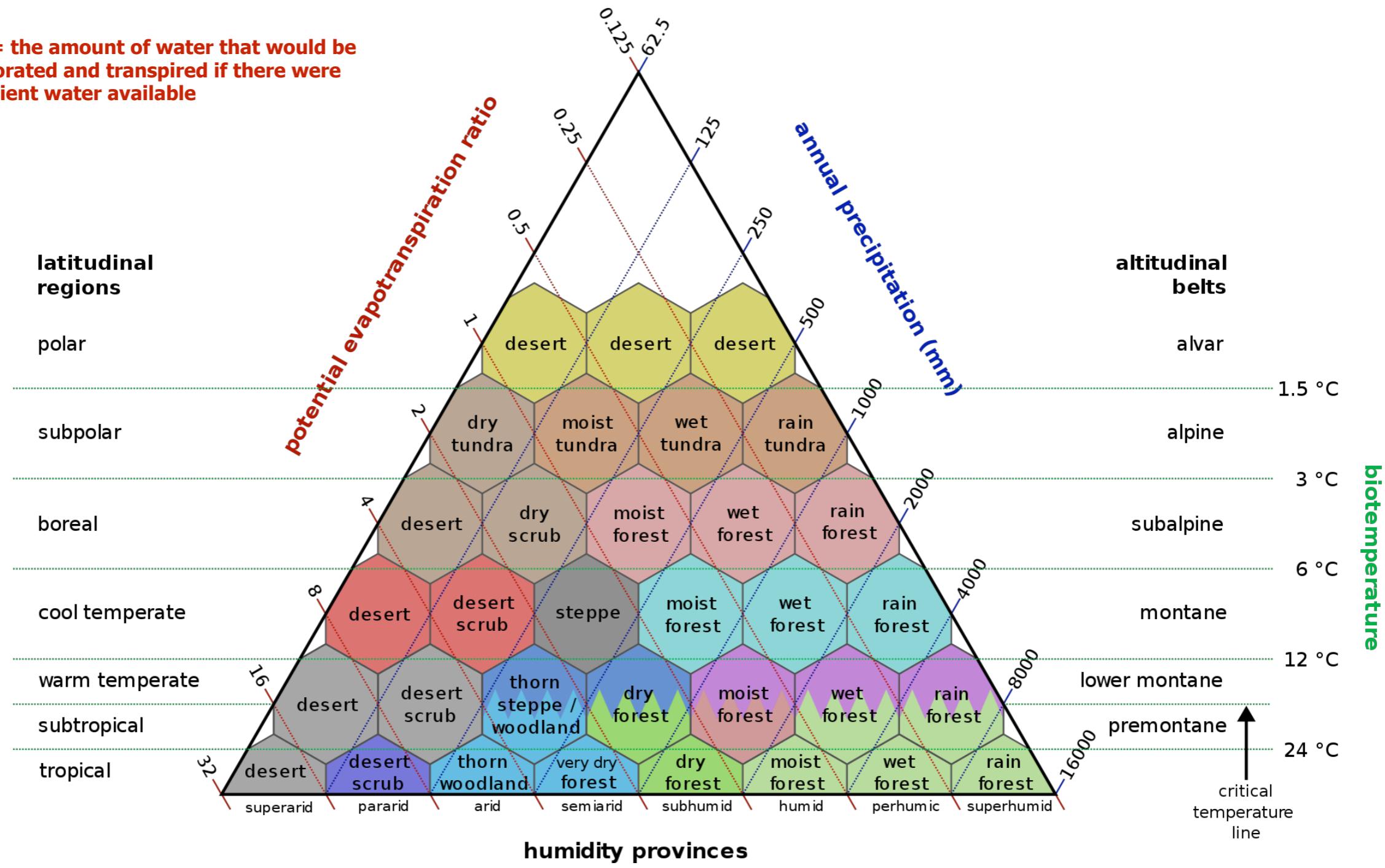
Global biomes



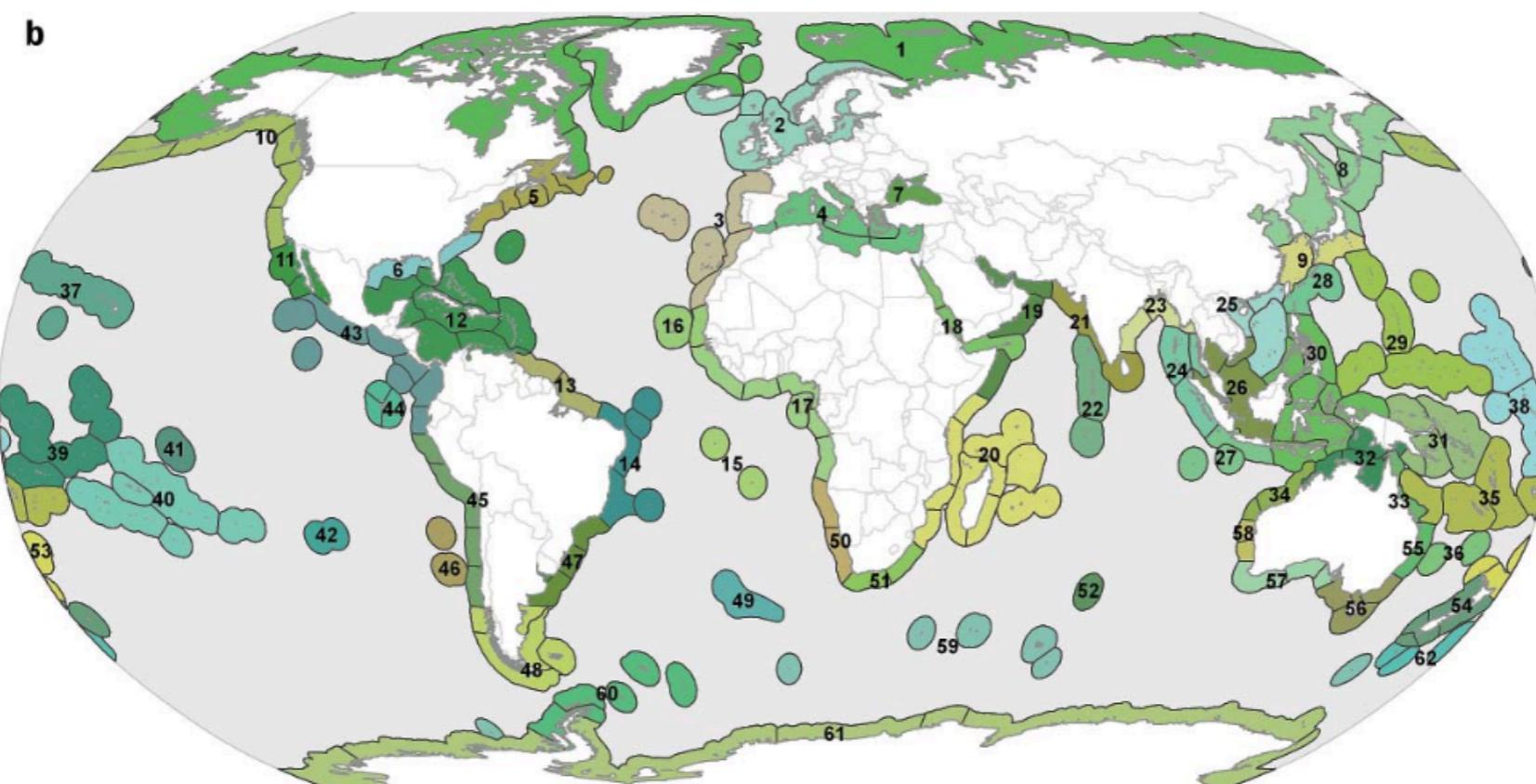
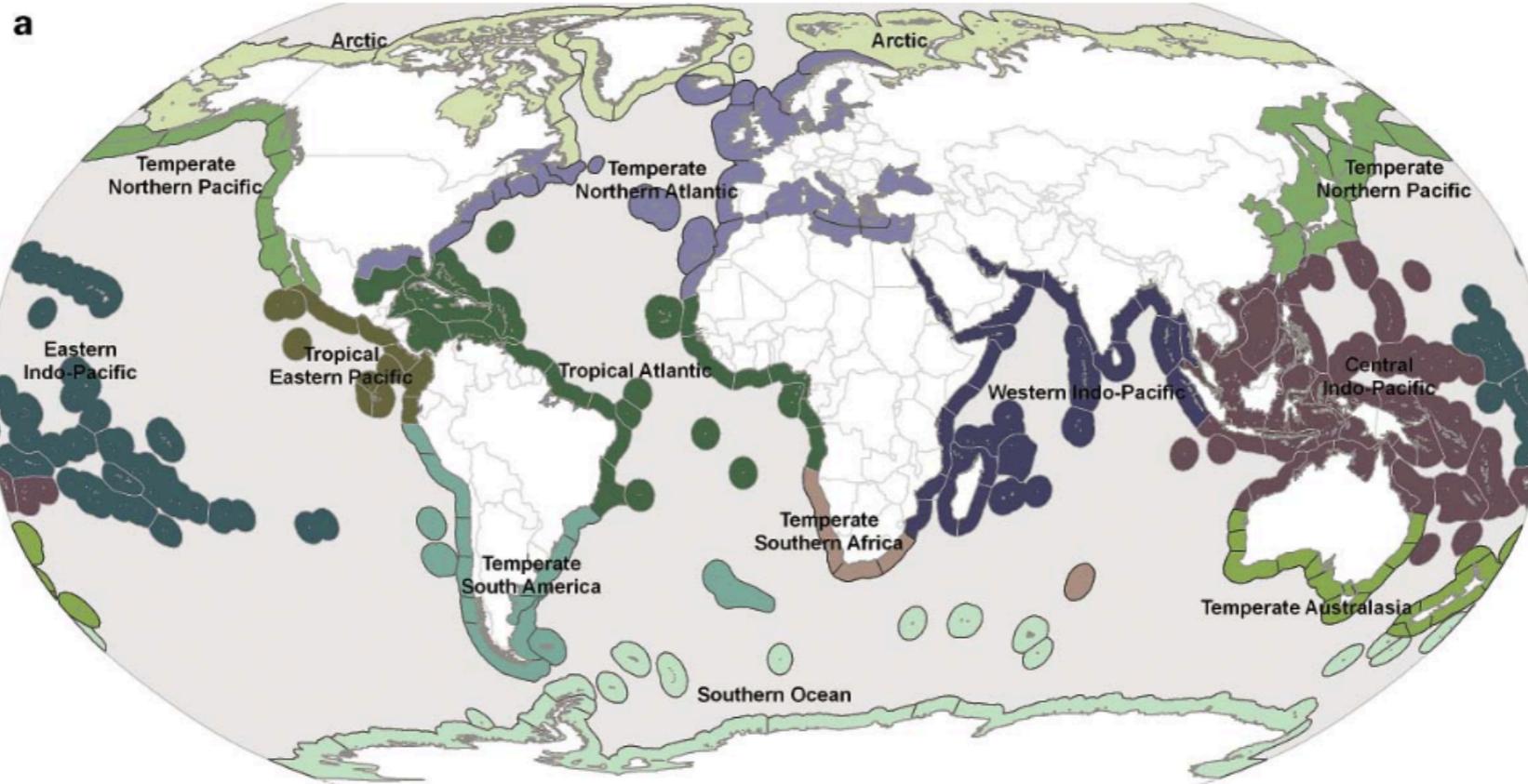
Holdridge Life Zones

low PET ratio is where evaporation greatly exceeds transpiration

PET = the amount of water that would be evaporated and transpired if there were sufficient water available



Marine Ecoregions of the World (MEOW)



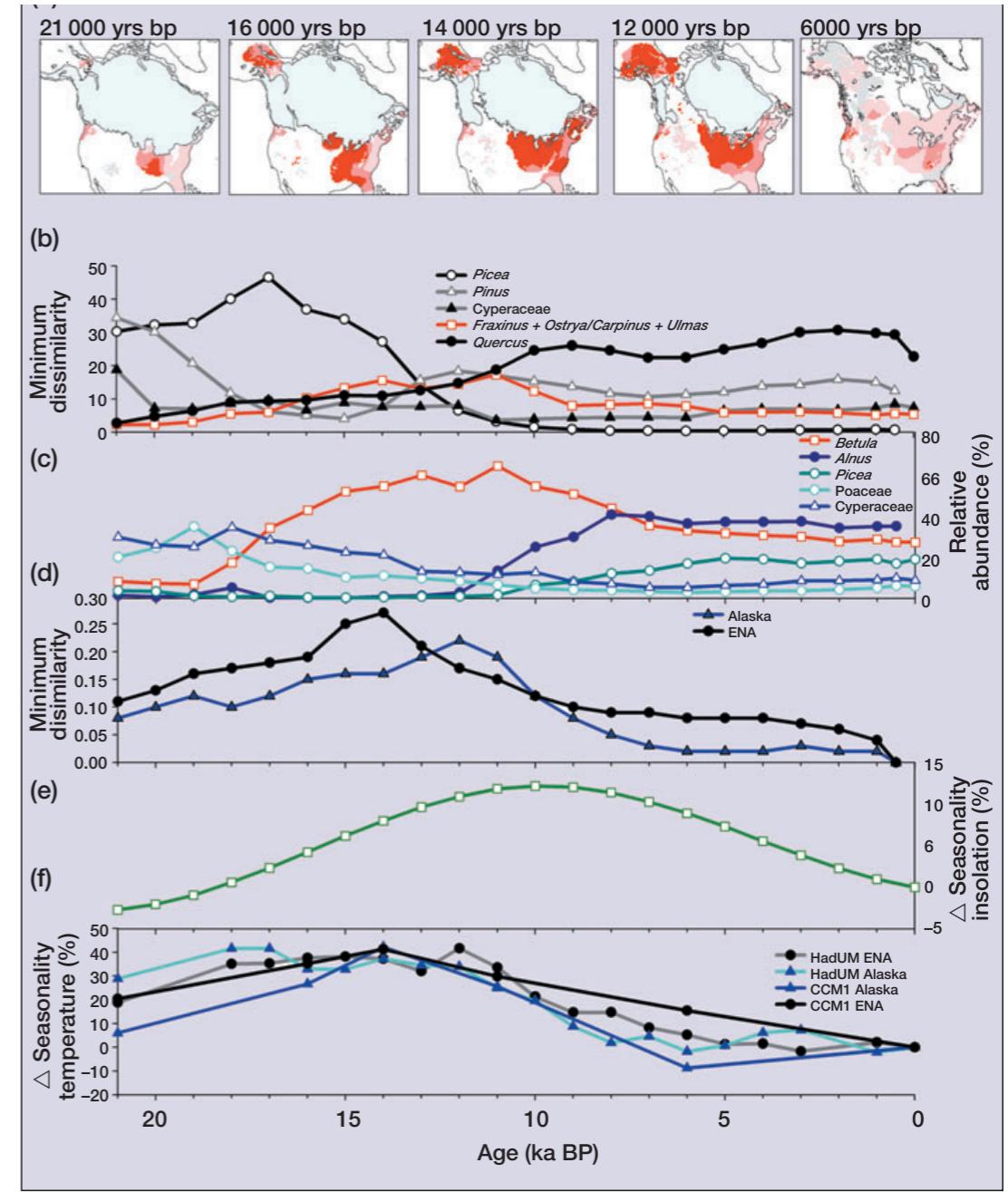
breaking the defined regions
based on biota and environmental
conditions

The Physical (abiotic) Template

"No-analog communities are defined by the existence of extant species in groupings that are not currently seen in modern biomes, or populations that have history of species assemblages that are no longer seen in the modern world."

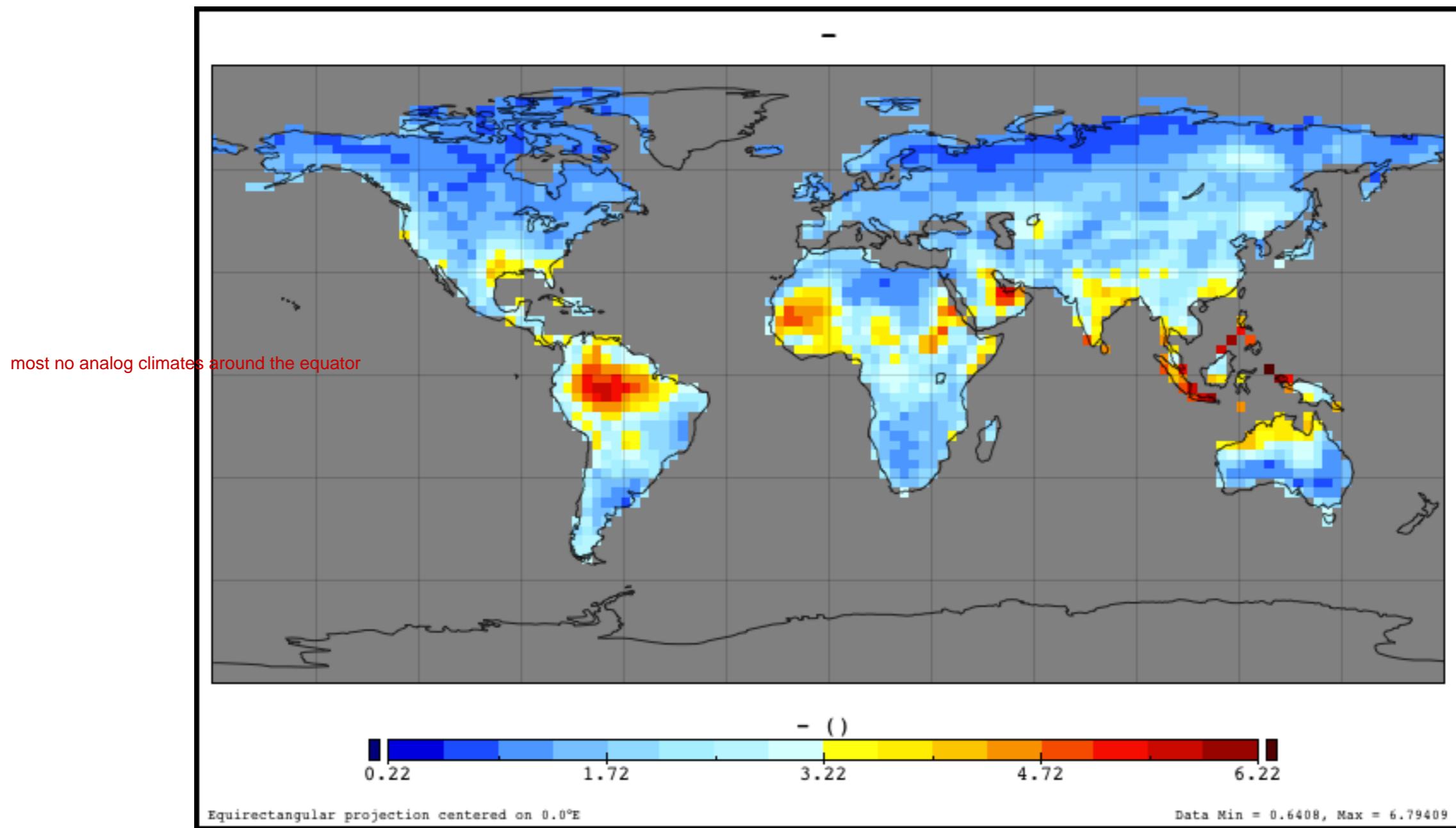
"No-analog" plant communities in North America (17,000-12,000 years ago):

- Most prevalent in Alaska and the interior of eastern North America (red shading in maps)
- Timing of peak no-analog communities in AK and eastern North America is similar, suggesting a common forcing.
- Likely candidate forcings include seasonality:
 - insolation (amount of solar energy)
 - temperature



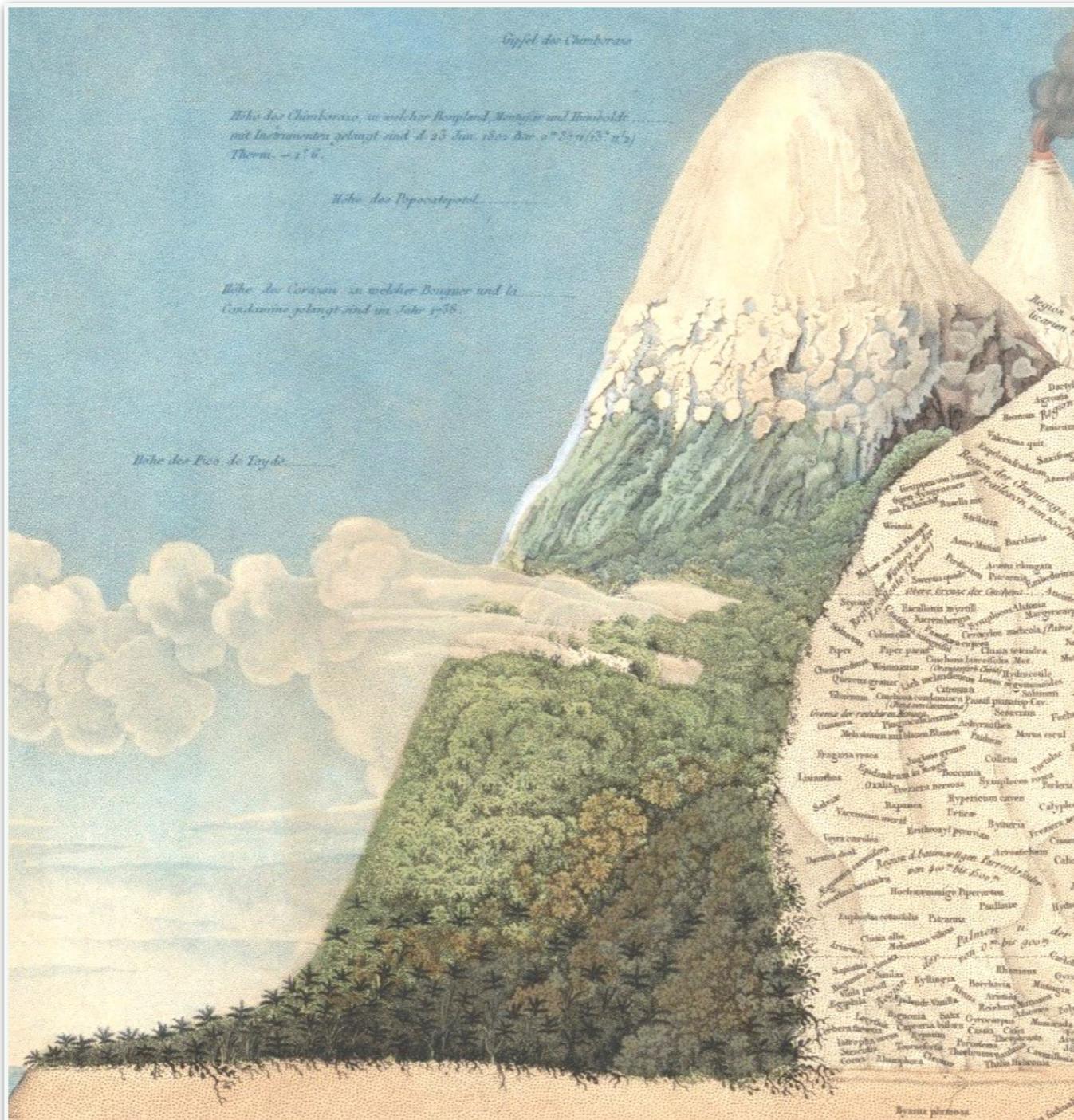
Williams & Jackson 2007

No-analog climates of the future



Williams et al. (2007)

Elevation gradients mimic latitudinal gradients

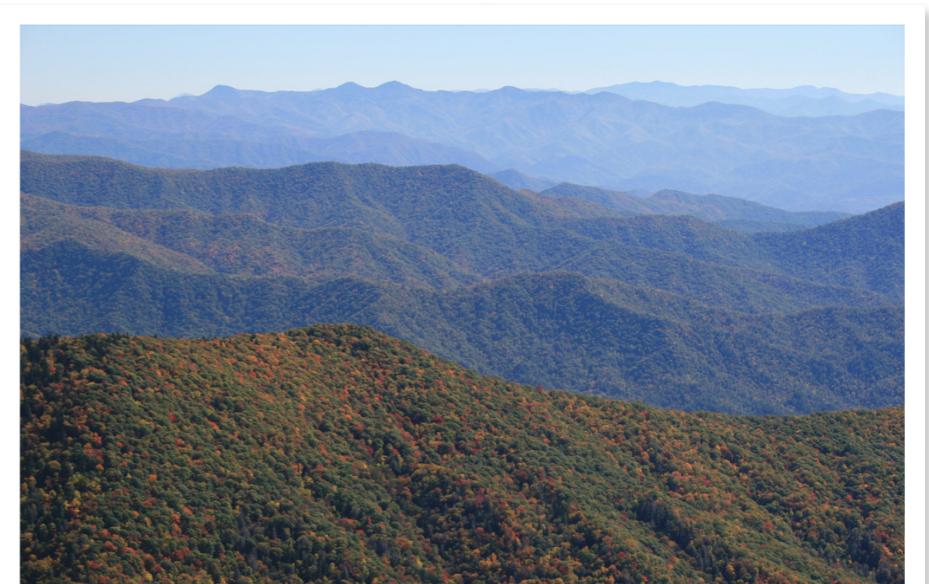


up in elevation moves from tropical forests to boreal regions

elevation is often included as a predictor in models, but this is problematic because 3000m in one place is not equivalent to 3000m in another region. This means it is not a good predictor when trying to predict new climates.

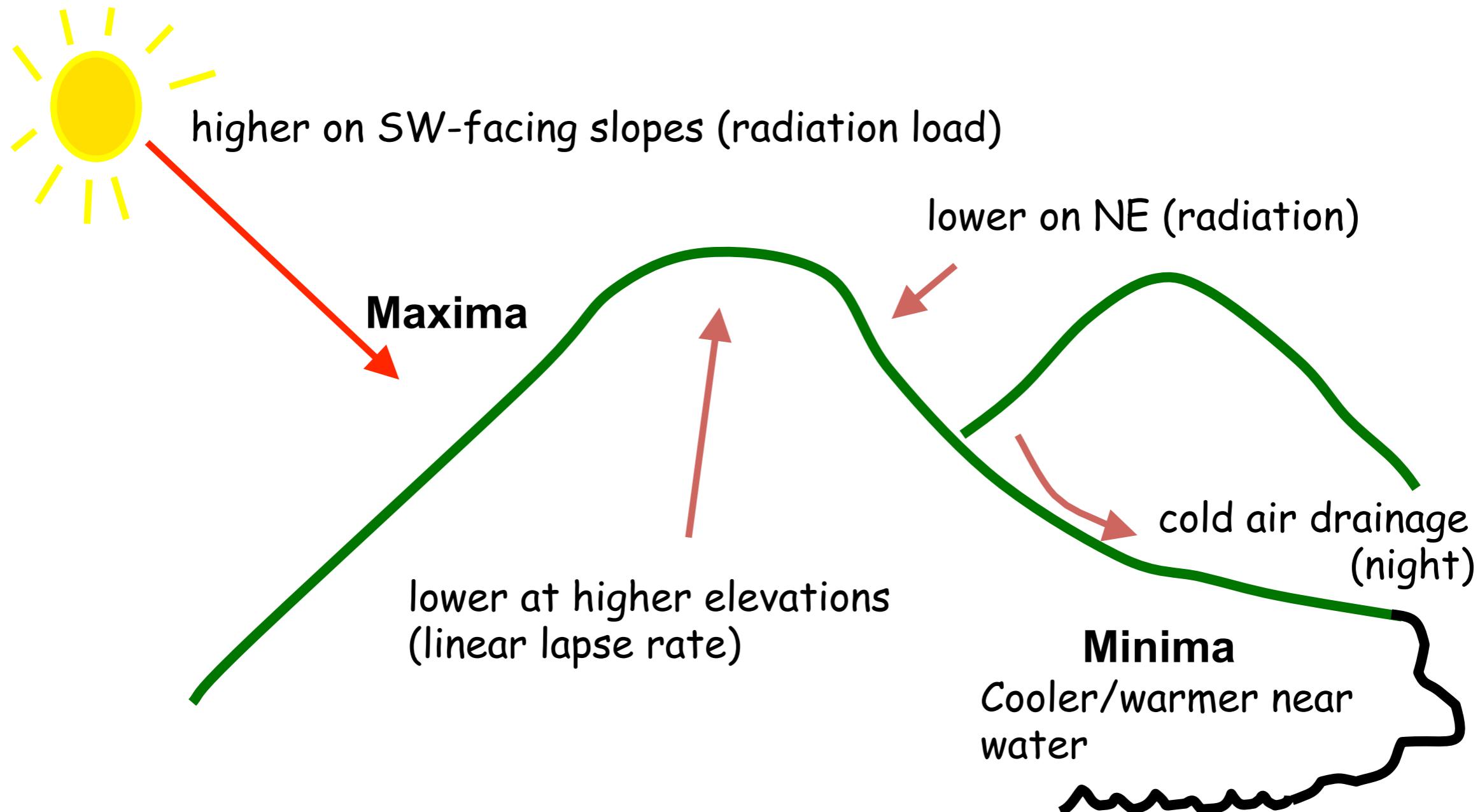
Landform

- **Landform** - geomorphic features affecting physical relief, soil development, and exposure
- Local elevation, aspect, parent material, and slope *modify the effects of climate*
 - alter air & ground temperature, quantities of moisture, nutrients, etc. available at sites within a landscape
 - southwest facing slopes receive more solar radiation than north facing slopes, resulting in warmer & drier conditions
 - affect the flow of organisms, propagules, energy, and material
 - influence frequency and spatial pattern of some forms of disturbance



for northern hemisphere!

Landform



Gradient Analysis

(Continuously varying environment without patchiness)

- Gradient analysis

1. Sample vegetation and environment (along elevation transect)
 2. Array samples according to species compositional trends
 3. Relate these trends to changes in the environment
- Common patterns emerge:
 - Temperature trend (elevation)
 - Moisture trend (local terrain)
 - Energy (exposure trend)
 - Soils or parent material

moisture trends are complicated by moisture pooling in valleys
all of the environmental factors tie into the resulting soil and parent material

Great Smokey Mountains National Park

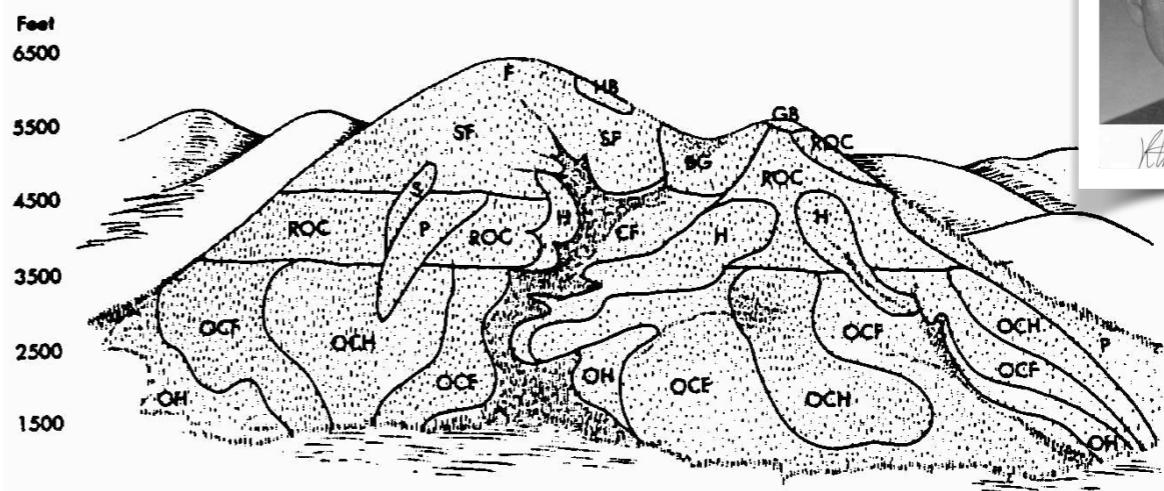
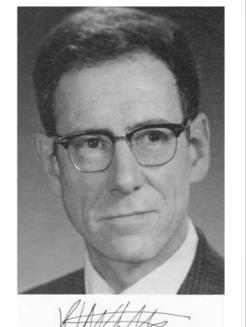


Figure 10.9. Topographic distribution of vegetation types on an idealized west-facing mountain and valley in the Great Smoky Mountains. Vegetation types: BG, beech gap; CF, cove forest (darker shading indicates steep slopes); F, Fraser fir forest; GB, grassy bald; H, hemlock forest; HB, heath bald; OCF, chestnut oak-chestnut forest; OCH, chestnut oak-chestnut



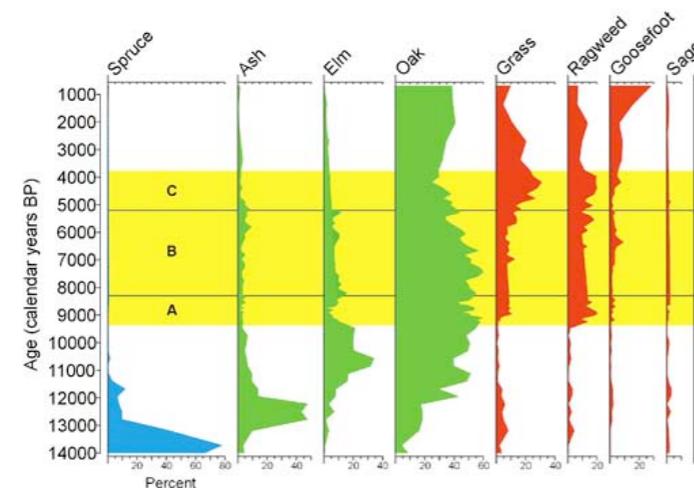
Whittaker 1956

Climate change will alter environmental gradients

Why do we model individual species responses to climate change instead of plant communities?

individual species respond differently
past assemblages do not always resemble present

Chatsworth Bog, Illinois



Where hickory forests assemble and disassemble depends on where individual species tend to overlap and result in the community

Great Smokey Mountains National Park

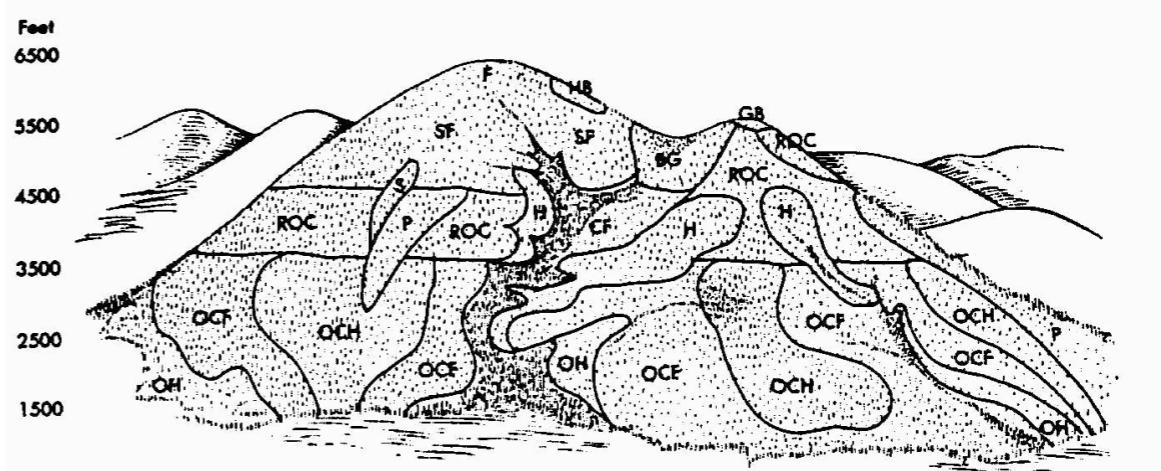
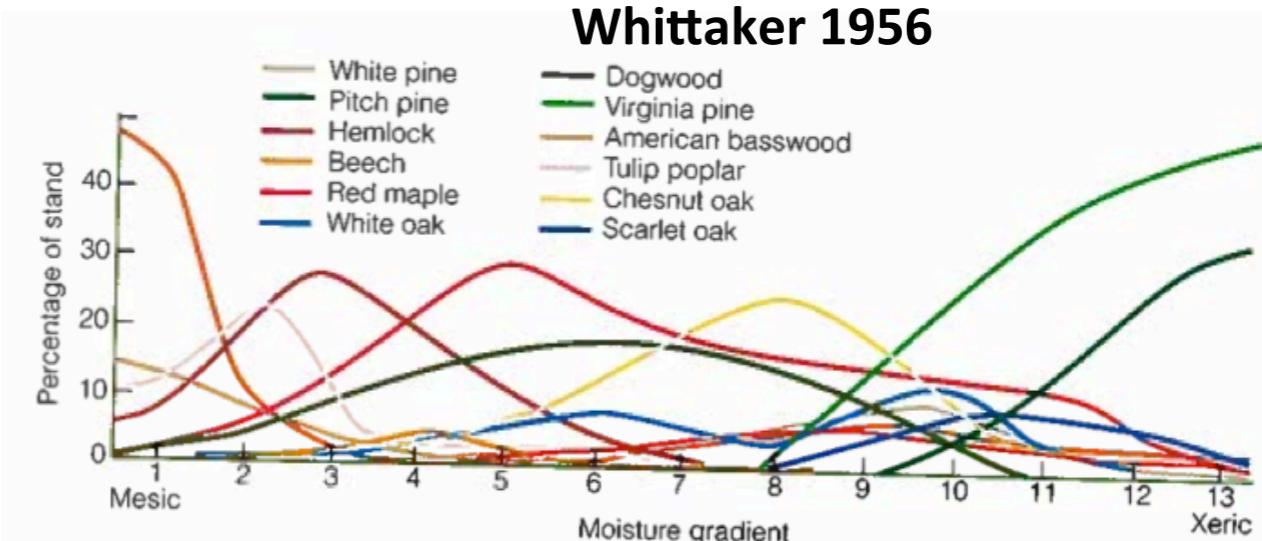
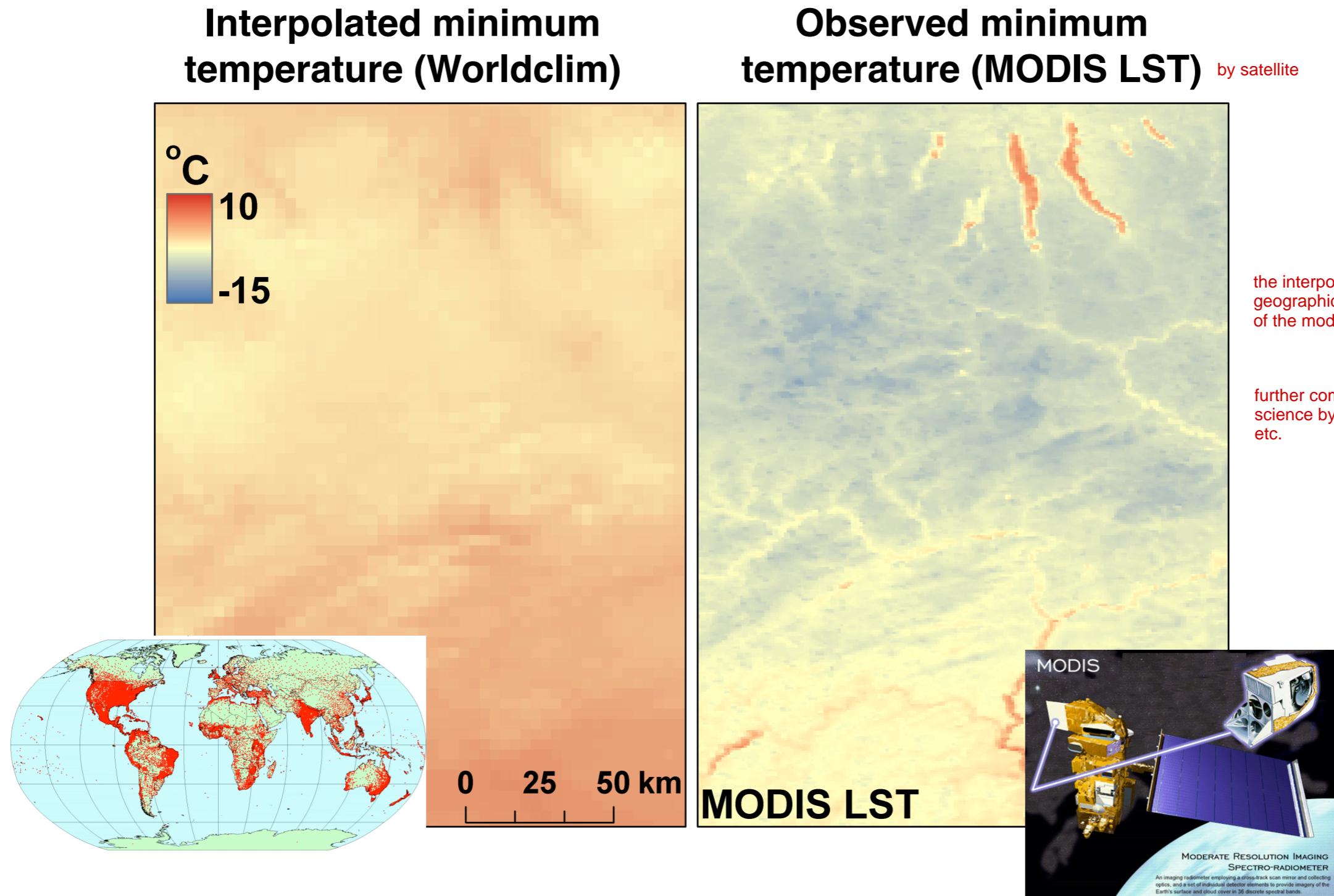


Figure 10.9. Topographic distribution of vegetation types on an idealized west-facing mountain and valley in the Great Smoky Mountains. Vegetation types: BG, beech gap; CF, cove forest (darker shading indicates steep slopes); F, Fraser fir forest; GB, grassy bald; H, hemlock forest; HB, heath bald; OCF, chestnut oak—chestnut forest; OCH, chestnut oak—chestnut heath; OH, oak-hickory forest; P, pine forest and pine heath; ROC, red oak—chestnut oak; S, spruce forest; SF, spruce-fir forest; WOC, white oak—chestnut forest. (from "Vegetation of the Great Smoky Mountains," by R. H. Whittaker, 1956, Ecological Monographs 26, 1-80. Copyright by Ecological Society of America, reprinted by permission.)

Whittaker 1956

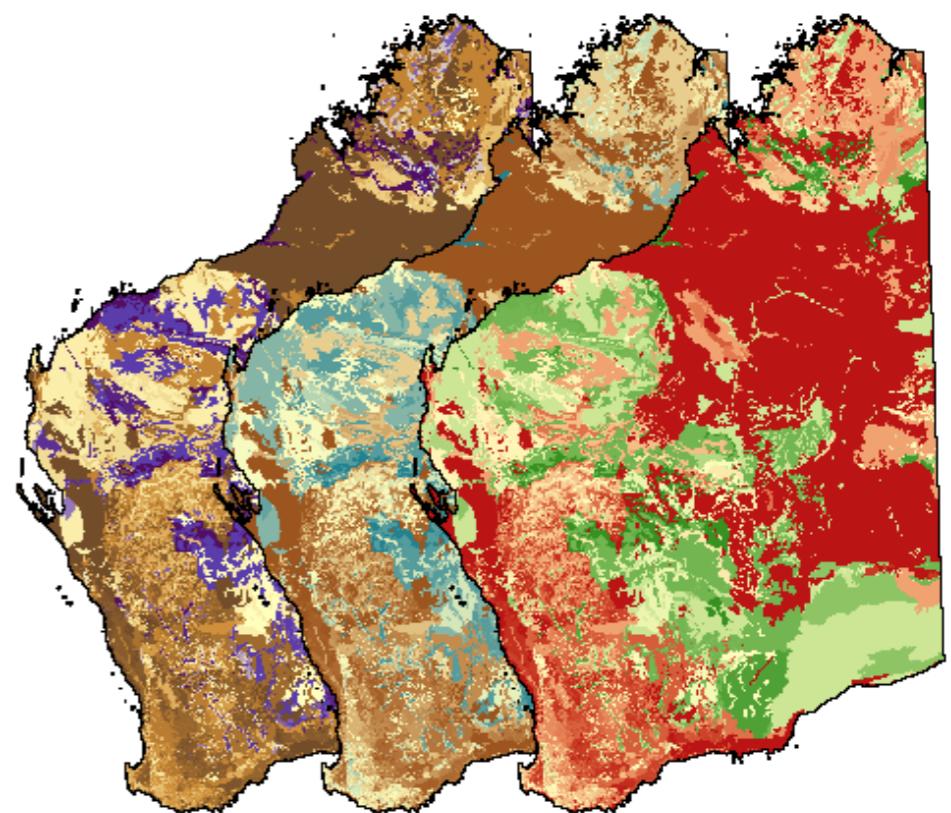


Quantifying abiotic gradients



Soils

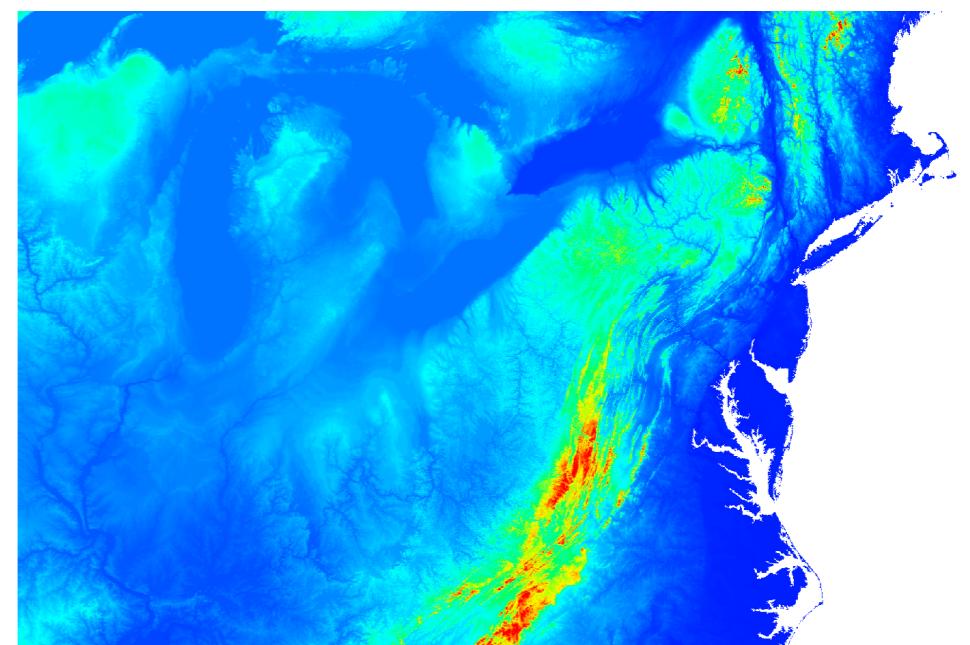
- Provide nutrients, moisture, support (terrestrial)
- Impact water quality, groundwater, stream flow
- vary across scales, from local to regional as a function of parent material, climate, vegetation, landform, disturbance



Terrain Indices

- Terrain modeling is an active area of research in landscape ecology
 - Analogous to mapping pattern indicators
 - Calculation requires digital elevation data (DEM)
 - Provides *continuous* rather than categorical classification
 - Ecological processes often constrained by topography

Digital elevation model (DEM)

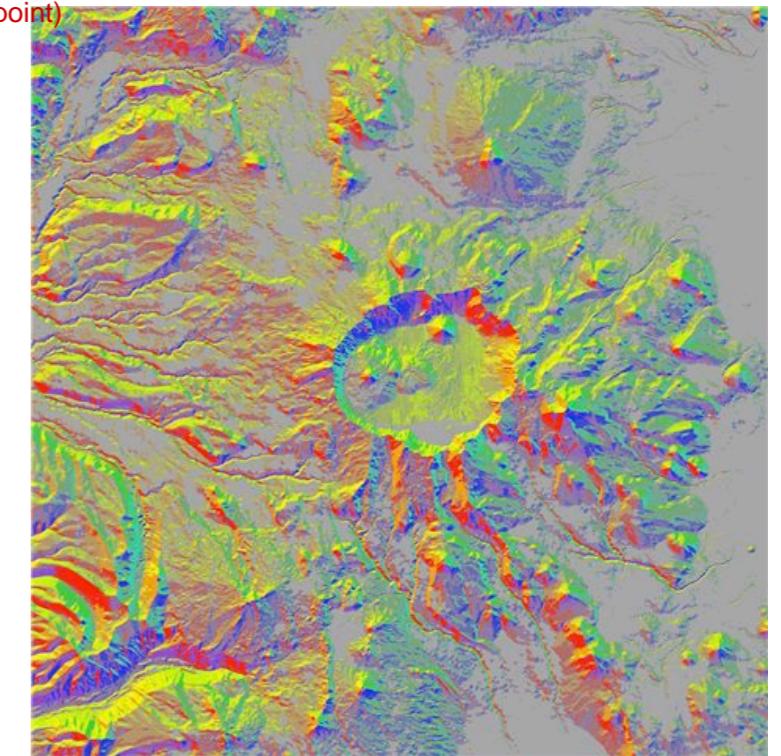


Terrain Indices: First order derivatives from digital elevation data

Slope and aspect

(cardinal direction influences the amount of solar radiation at that point)

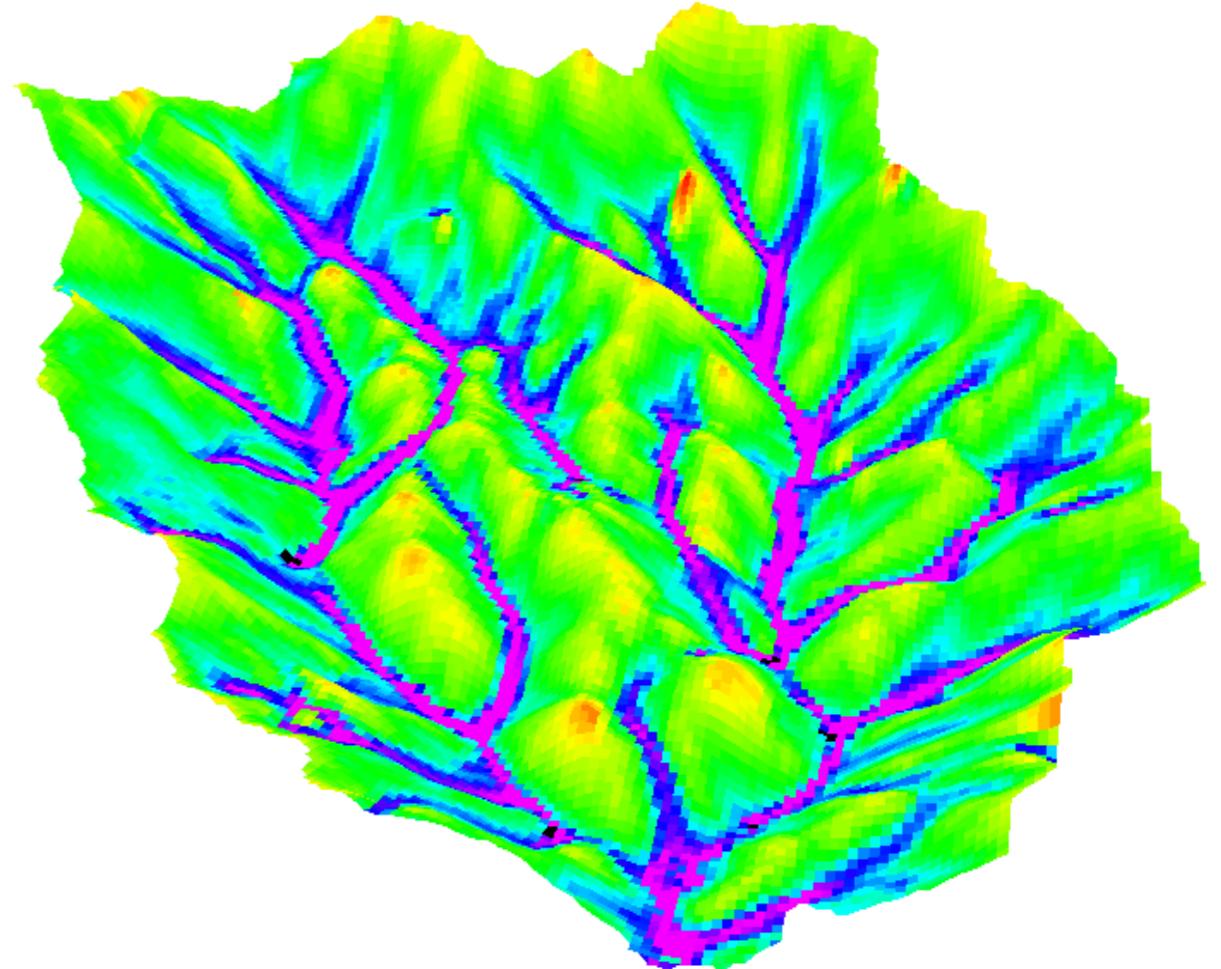
- slope defined as a plane tangent to the surface and has 2 components:
 - slope gradient = range in altitude
 - slope aspect = compass direction of change
- units
 - slope gradient: %, degrees, radians
 - aspect: degrees (compass bearing)
- Sensitive to grain & extent...and often correlated



Soil Water Balance (W) = water supply (S) – water demand (D)

South facing= water demand exceeds supply

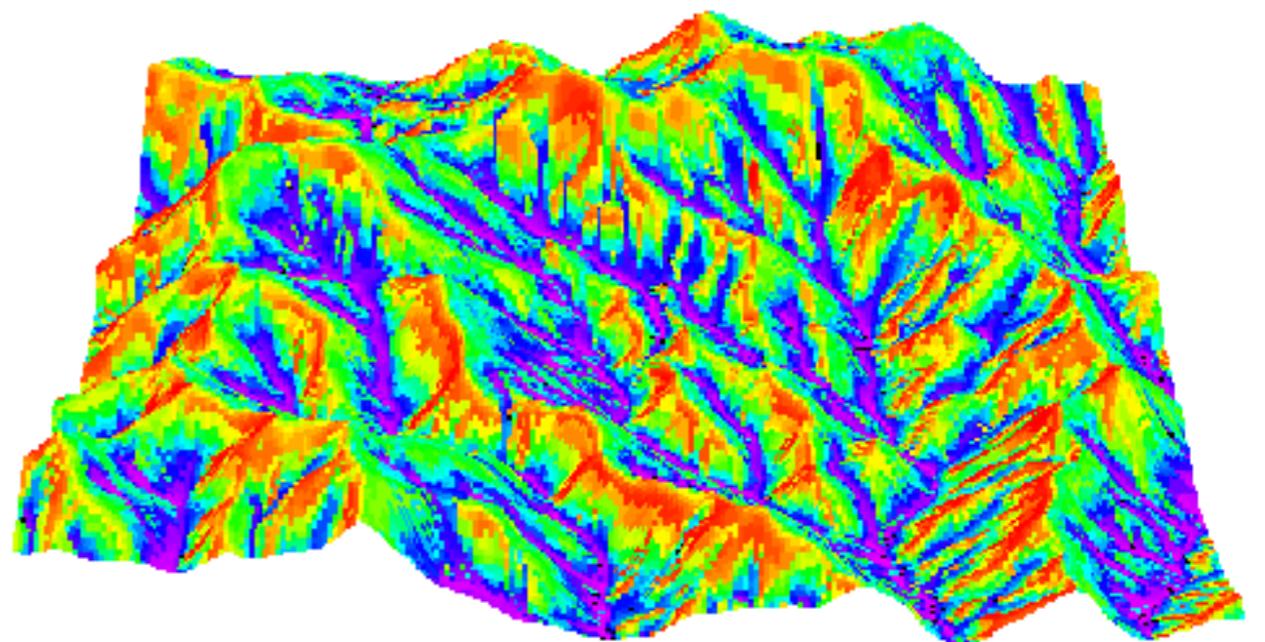
- Balance between water supply
- Supply = inputs (precip, drainage) \pm storage (soil texture, depth)
- Demand = f (temperature, radiation, vegetation)
- Excellent illustration of the way in which physical factors interact to generate complex environmental gradients



Topographic Relative Moisture Index (TRMI)

Summed scalar index

- Aspect
- Slope
- Curvature
- Relative slope position



Disturbance

Discrete event in time that disrupts ecosystem, community, or population structure, changes resource availability, substrate, or the physical environment

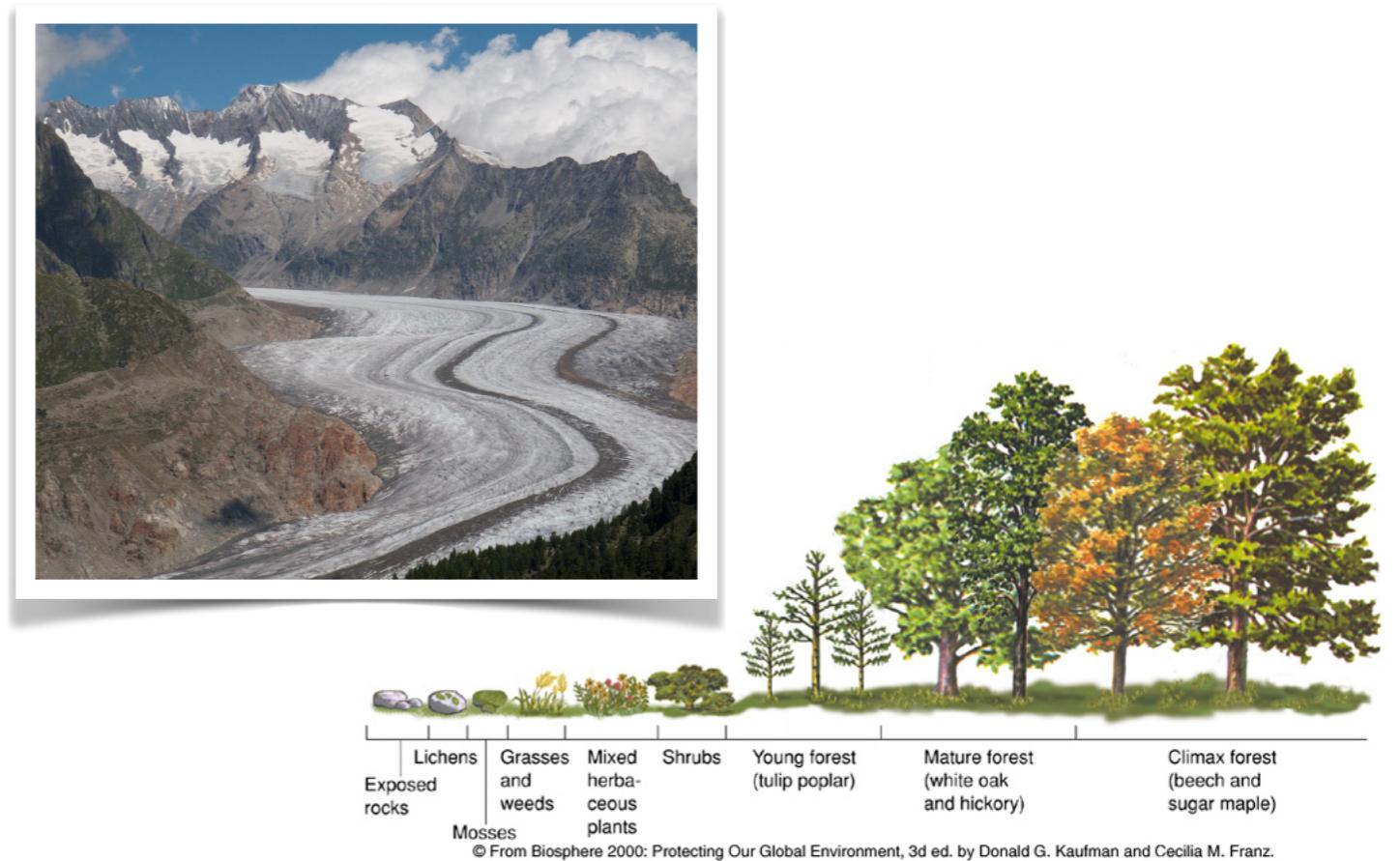
- Fire, floods, storms, volcanic eruptions, wave action, etc
- Defined by their spatial distribution & extent, frequency, duration, and magnitude
- Can be influenced by vegetation pattern, landform, etc.



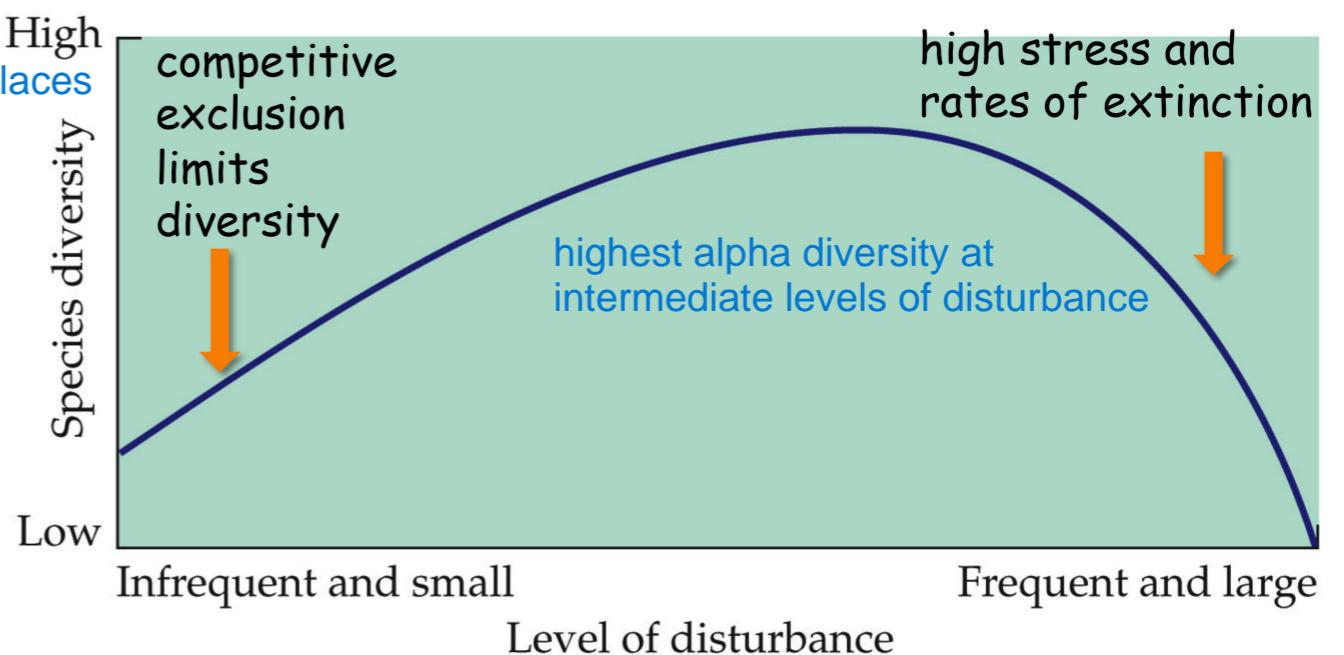
Disturbance

- Recovery from disturbance creates a mosaic of patches of different age (succession)
- Increases beta diversity
- Alters alpha diversity (intermediate disturbance hypothesis)

beta diversity= the difference in species composition between places



high disturbance only quick colonizers and disturbance tolerant species survive



Disturbance

plant pathogen killed trees in Australia



Biotic processes can interact with global change to act as disturbances at broad spatial scales, which in turn can interact with other disturbance processes

pine bark beetles killed large amounts of trees leaving them susceptible to fires

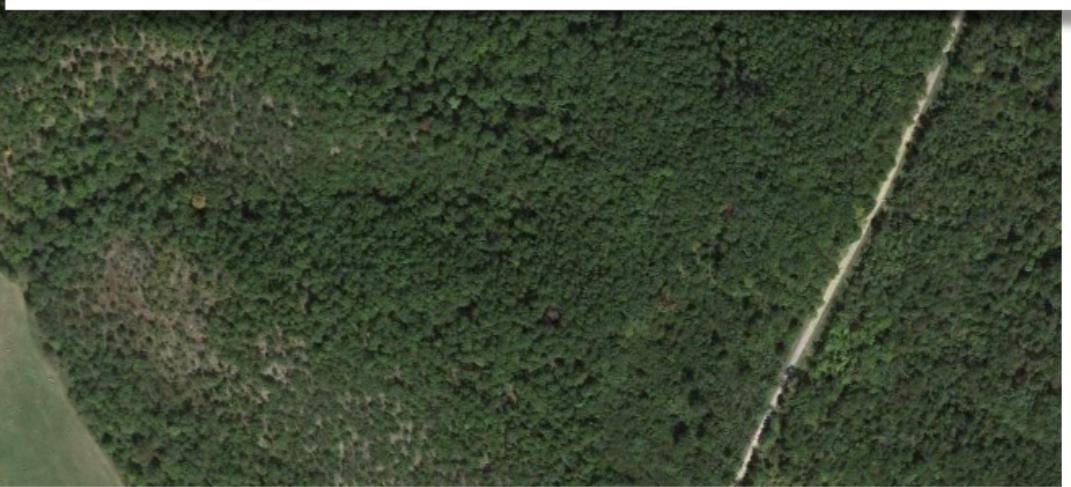


dead hemlock trees killed by woody adelgid



Shale barrens in western Maryland

warmer and drier making them more susceptible to fires
burning normally keeps out invasives, but less fires makes them susceptible



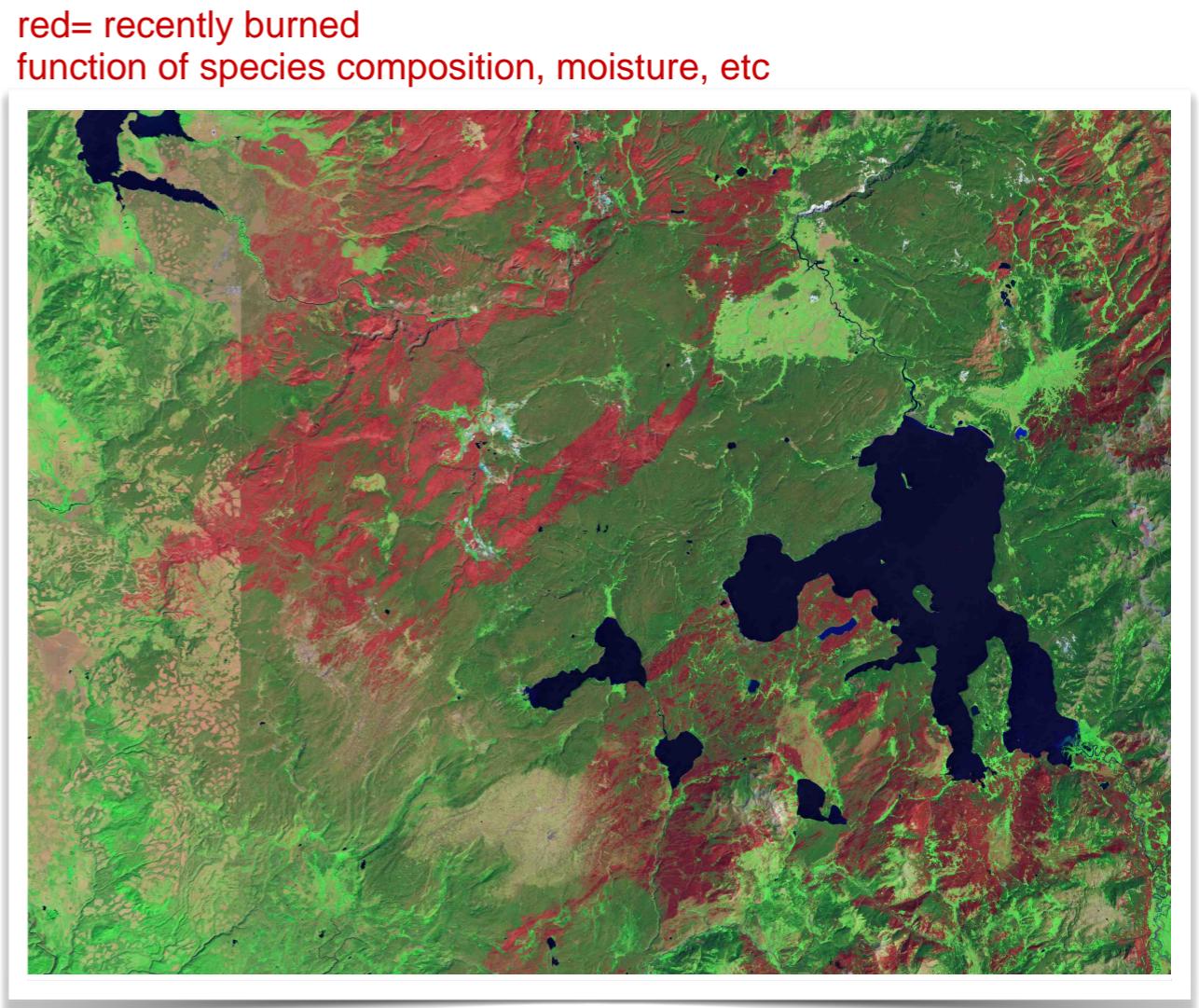
Land use

as a form of large spatial disturbance



Contingency & legacy effects

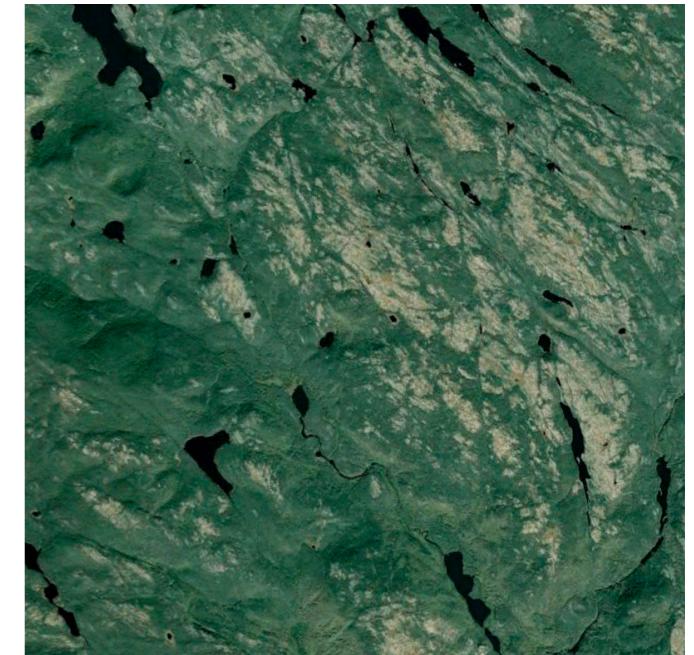
1. History is a result of and a determinant of vegetation patterns
2. Some of these effects are long lived, others are ephemeral - varies by landscape
3. Influence current trajectories
4. Effects discernible across a range of scales, but mainly at landscape level and below



The role of history in current landscape patterns: Example – Eastern deciduous forests

- Product of a long-term history of development on time scales of 1000 to millions of years
- Glacial cycles have had profound effects on the distributions and abundance of terrestrial plants
 - caused repeated disassembly and reassembly of forest communities
- During glacial intervals deciduous forests were restricted south of 33 deg and were greatly restricted in extent to favorable pocket refuges
- Ice sheets also greatly altered the physical template

ice sheet retreats on flat ground allows the trees to disperse vs in Europe, the Alps prevented species from moving across the landscape (happening much more slowly)

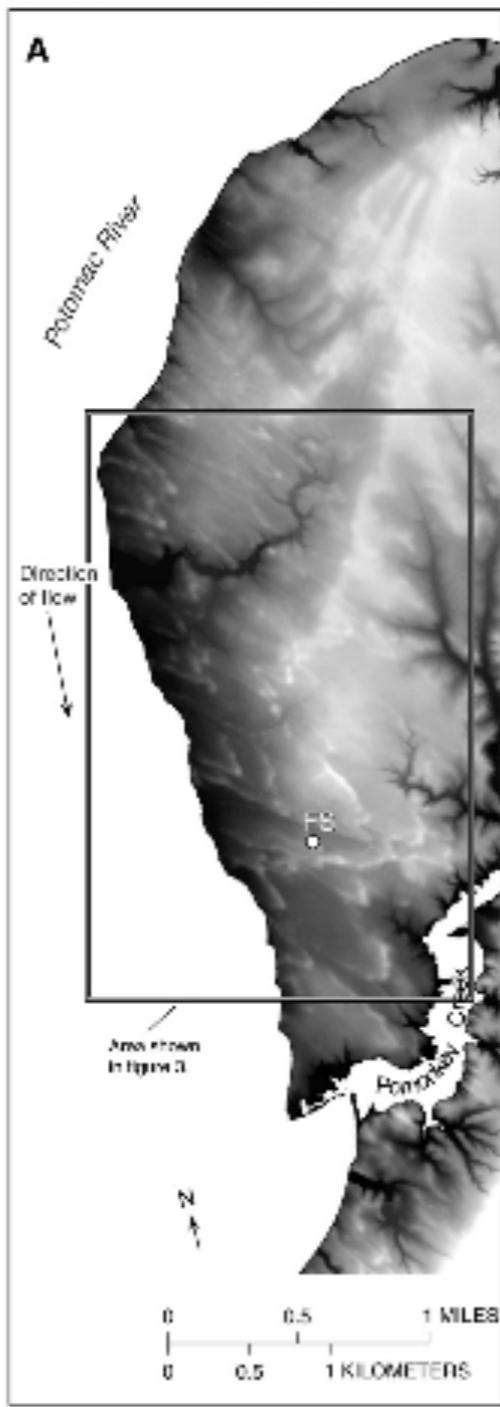


use pollen to reconstruct timeseries

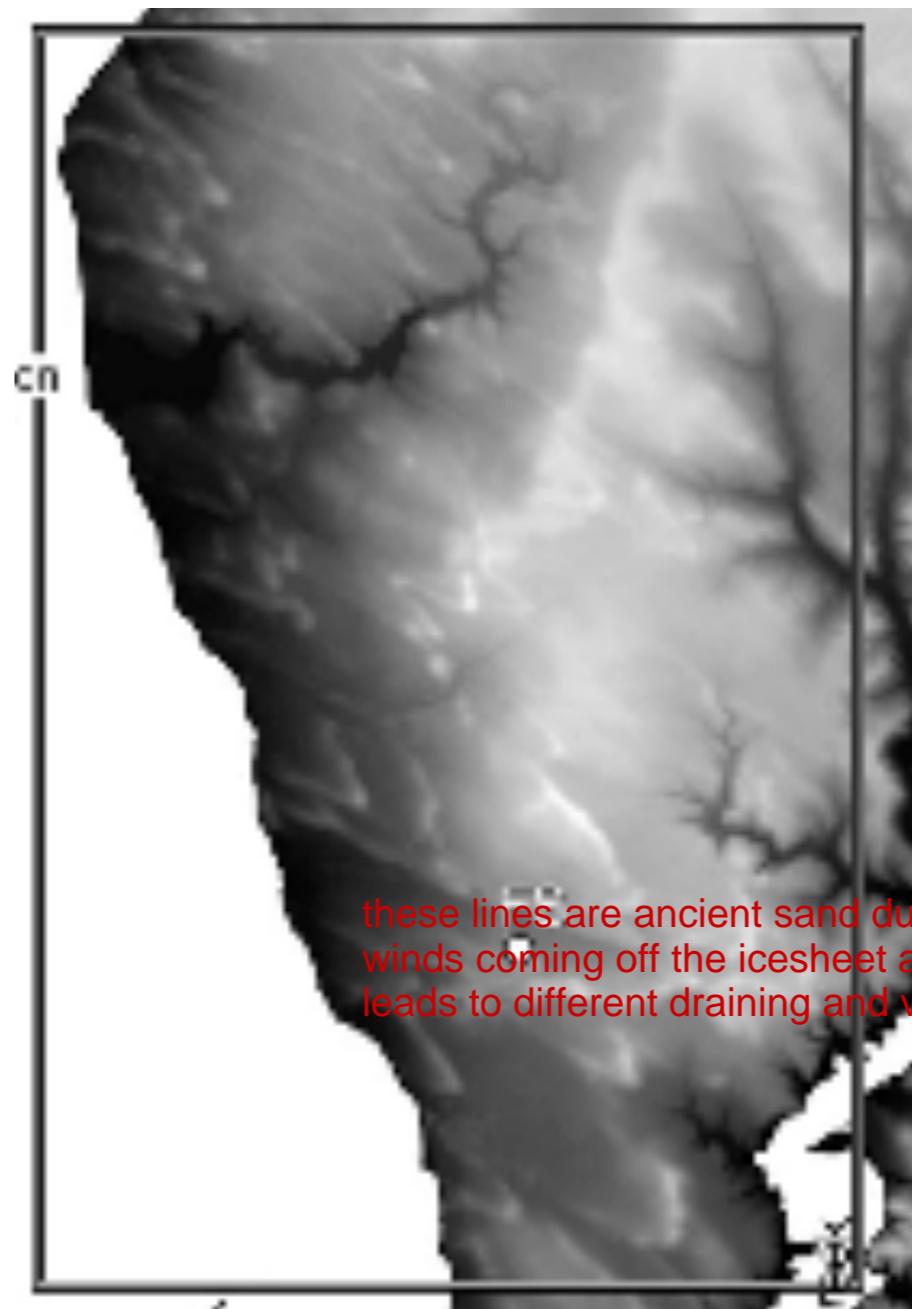


Delcourt & Delcourt 1989

The role of history in current landscape patterns: Example – Eastern deciduous forests



15-30k year old dunes in MD



gray shading is LIDAR digital elevation model

Markewich et al 2009

Biotic Processes

regeneration niche= seedlings need different conditions than adult plants

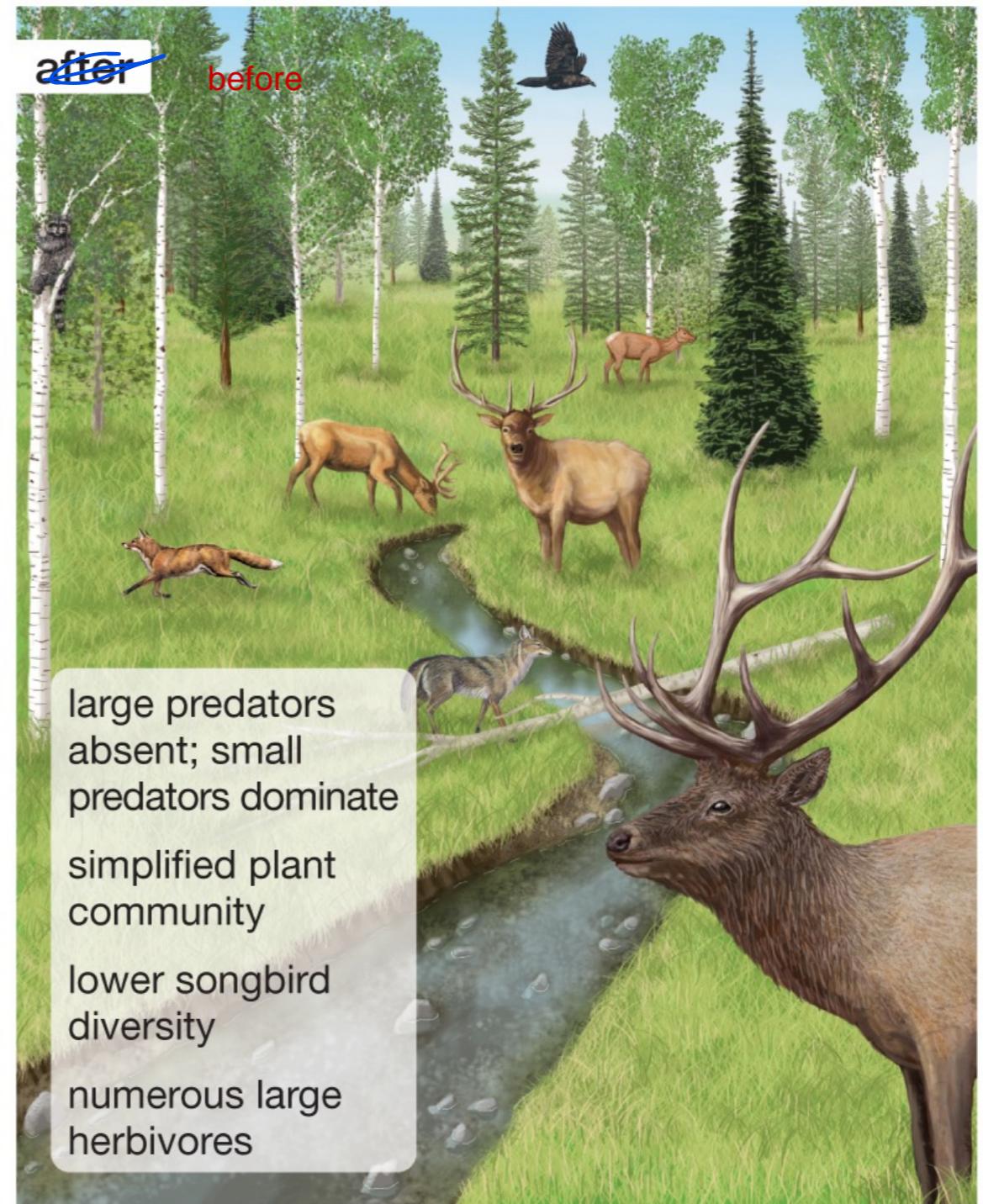
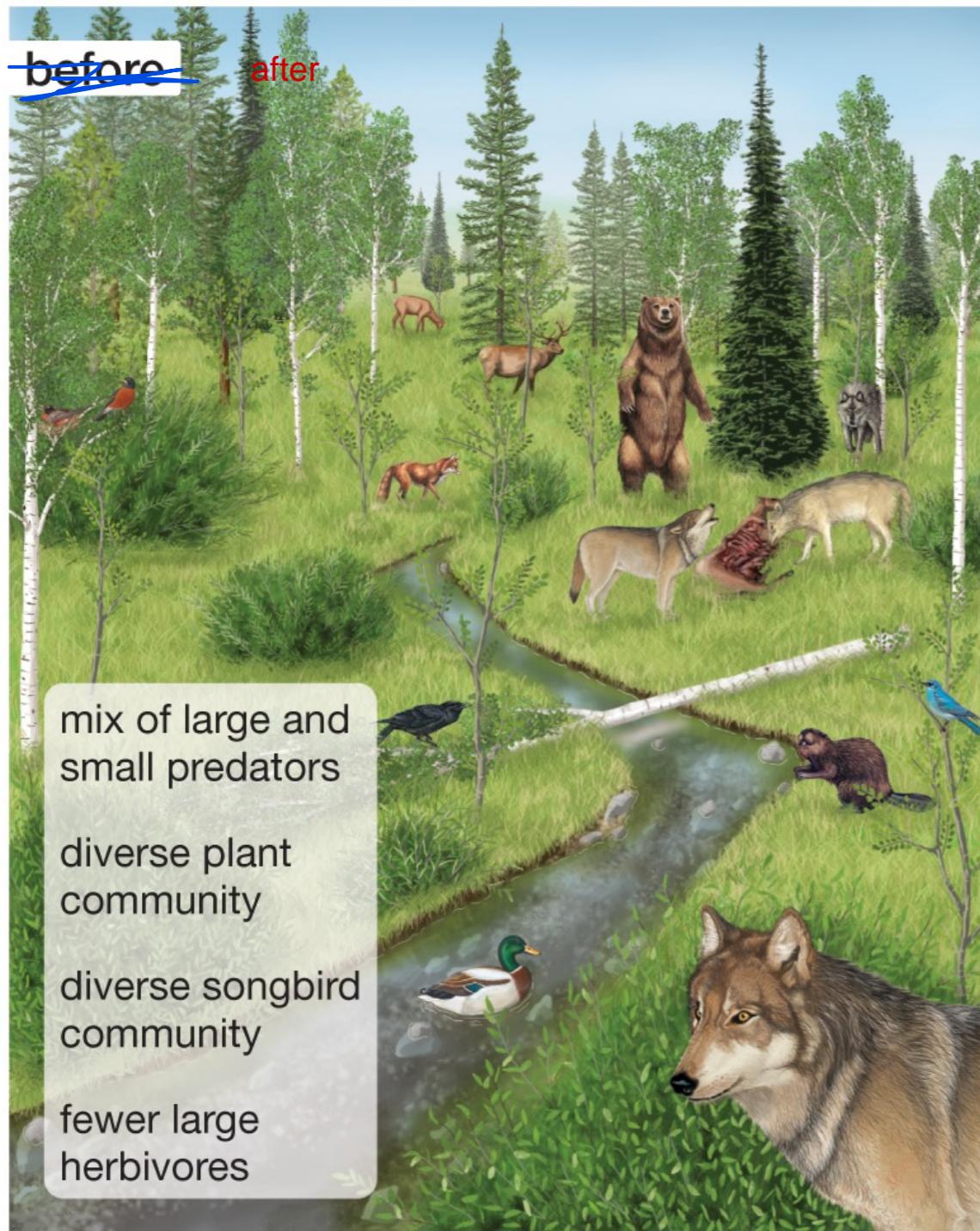
- **Establishment** – constraints are different for seedlings than established plants (regeneration niche)
- **Population Growth** – Differing responses of species to physical factors and resource gradients invokes competition as the primary mechanism for sorting species along gradients
- **Mortality** – multiple causes that operate at a variety of temporal and spatial scales
- **Dispersal** – complex, can reinforce existing patterns. Understanding of how dispersal interacts with the environment remains an active area of research



Biotic Processes - trophic cascades

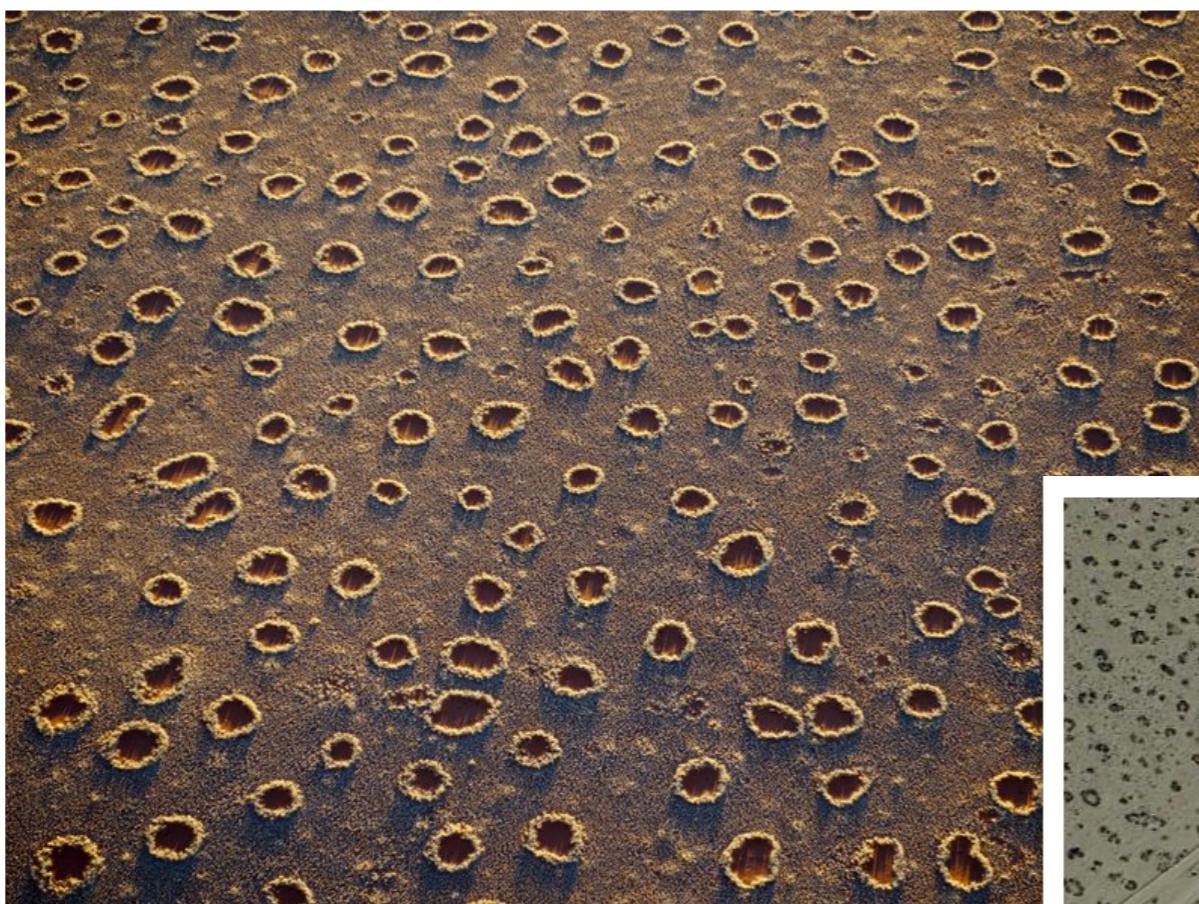
vegetation change after wolf reintroduction in Yellowstone

Trophic cascade scenario: top carnivore removal



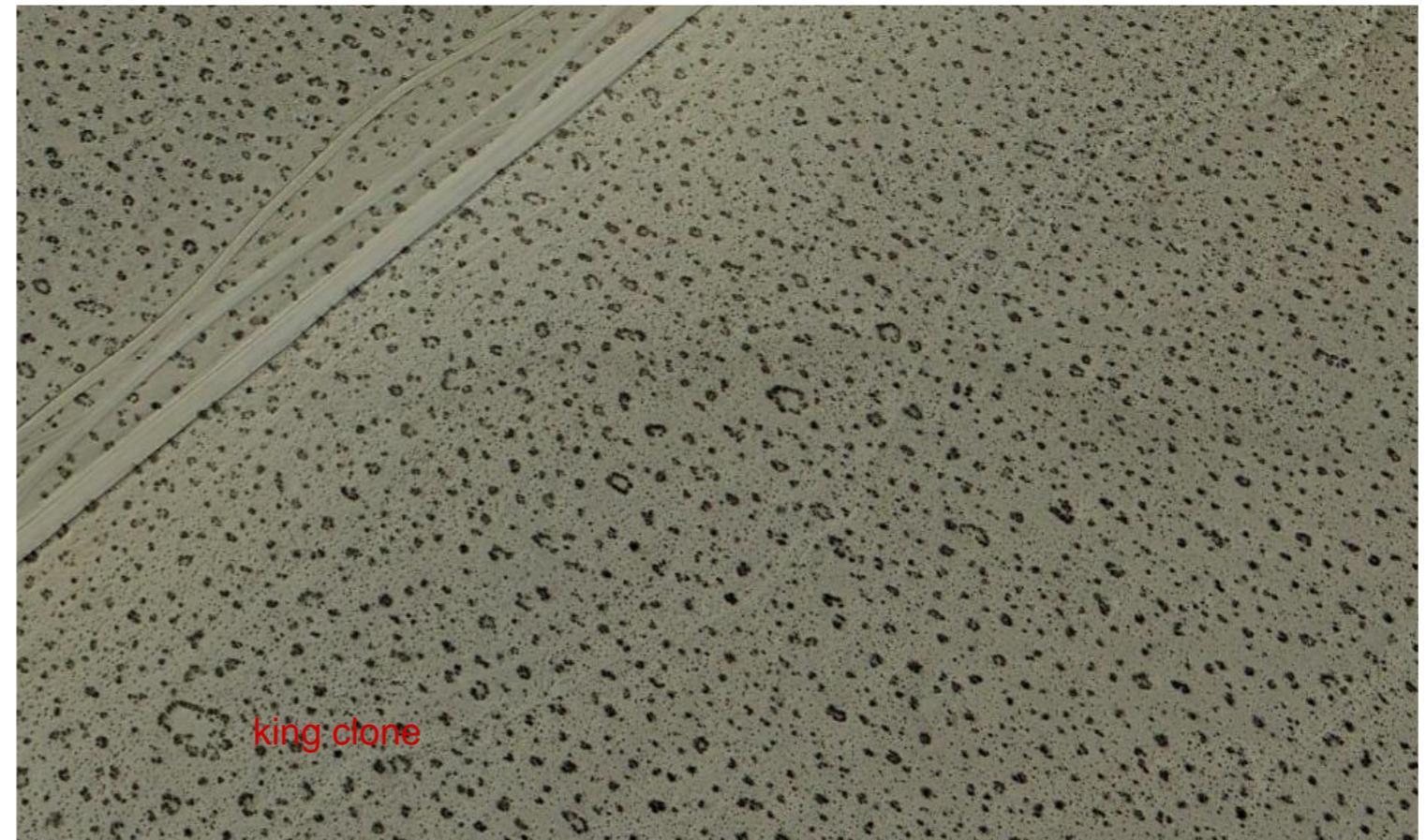
Biotic processes can generate complex patterns even in (relatively) homogeneous environments

interaction between three species: short grass, tall grass, ants or termites



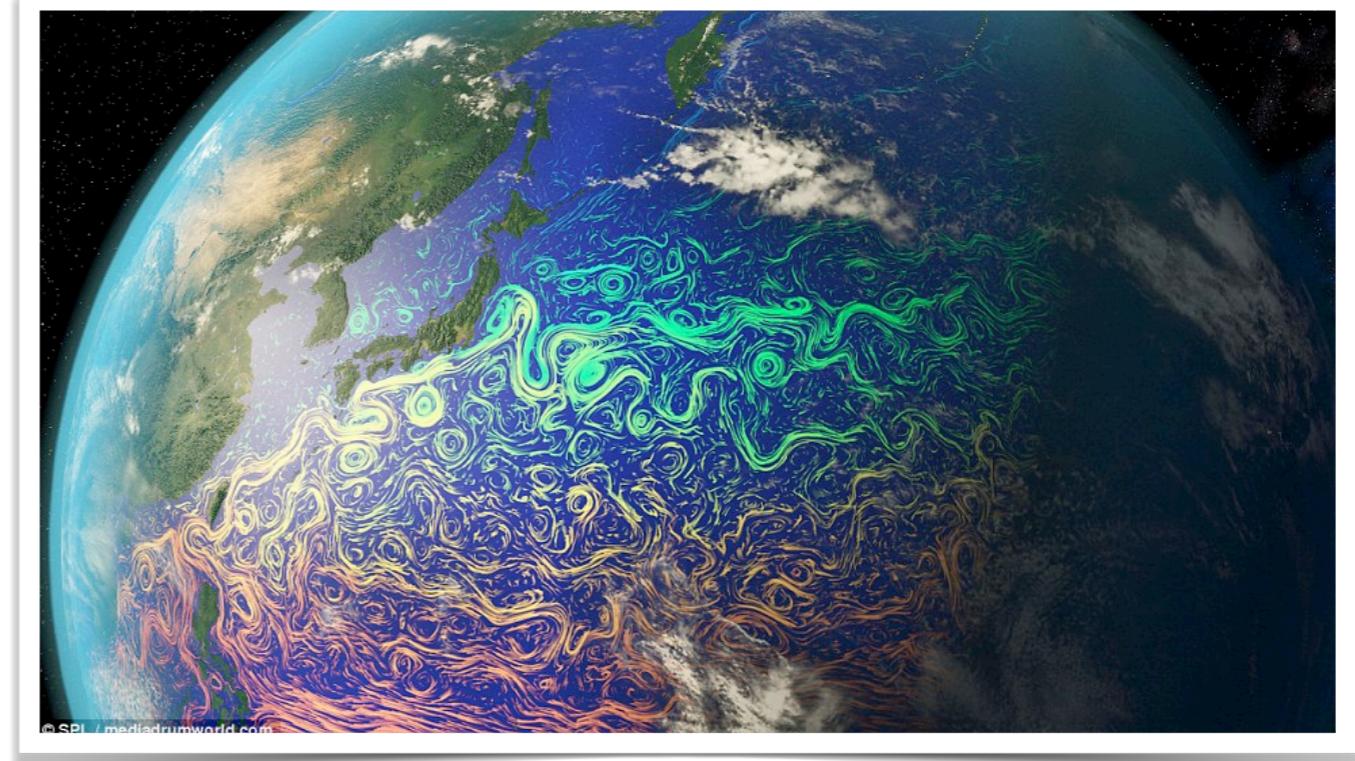
Fairy circles in Namibia

Creosote Bush - Mojave Desert
clones



Considerations for marine systems

- Greater challenges than in terrestrial systems
- Temporal rates of change can be much more rapid (compare forest patch mosaics to eddies with patches of entrained phytoplankton)
- Importance of chemical seascapes and soundscapes that generate spatial and temporal patterns & are modified by human activities



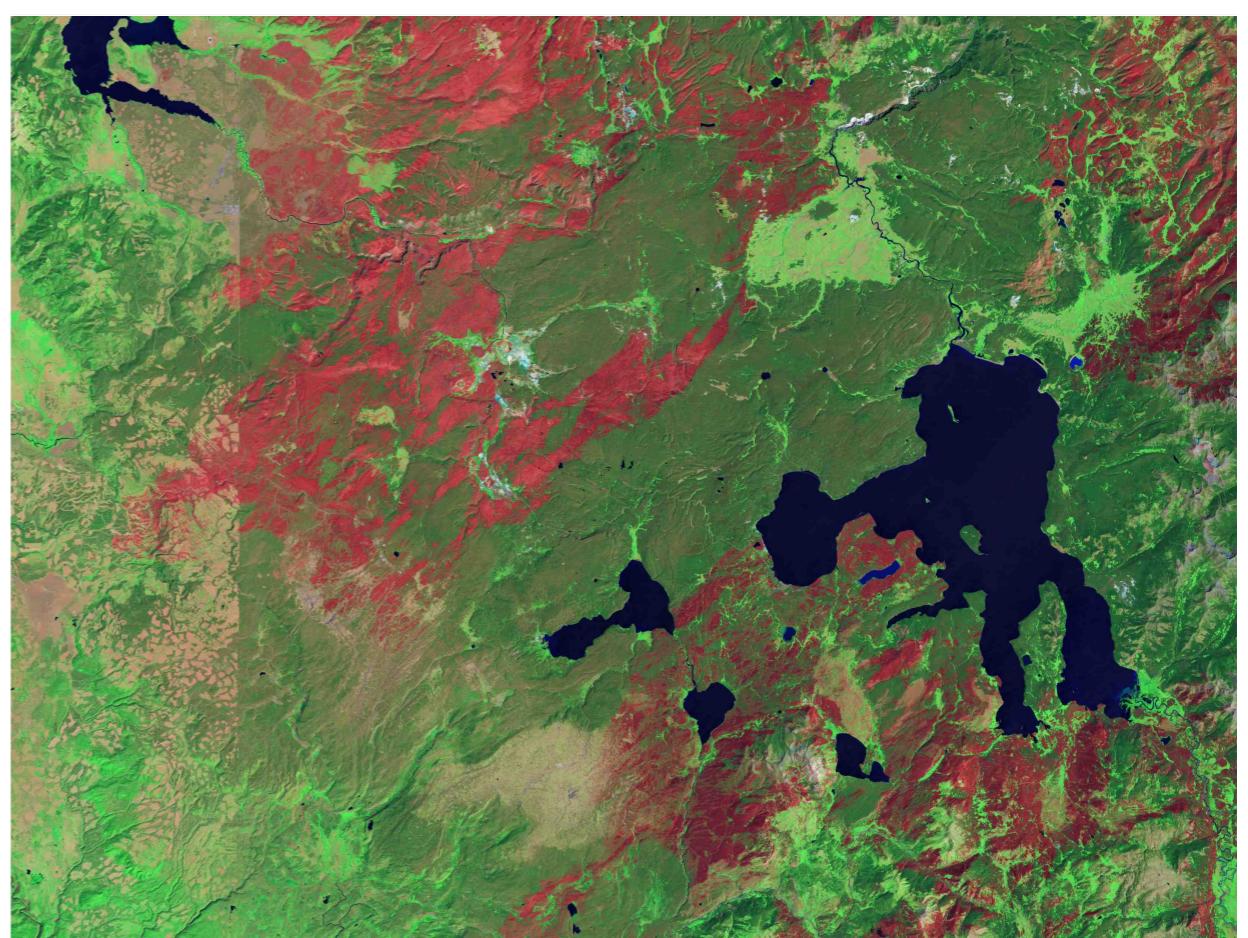
ie. chemical cues

Agents of spatial pattern - parting thoughts & confounding issues

Effects of multiple interacting drivers and controls on spatial patterns means that it is highly unlikely that any two landscapes are duplicated at any other **place or time**.

Multiple & contingent causation (spatial and temporal) allows for multiple outcomes, not a single deterministic result from a given set of initial conditions.

Every landscape is unique

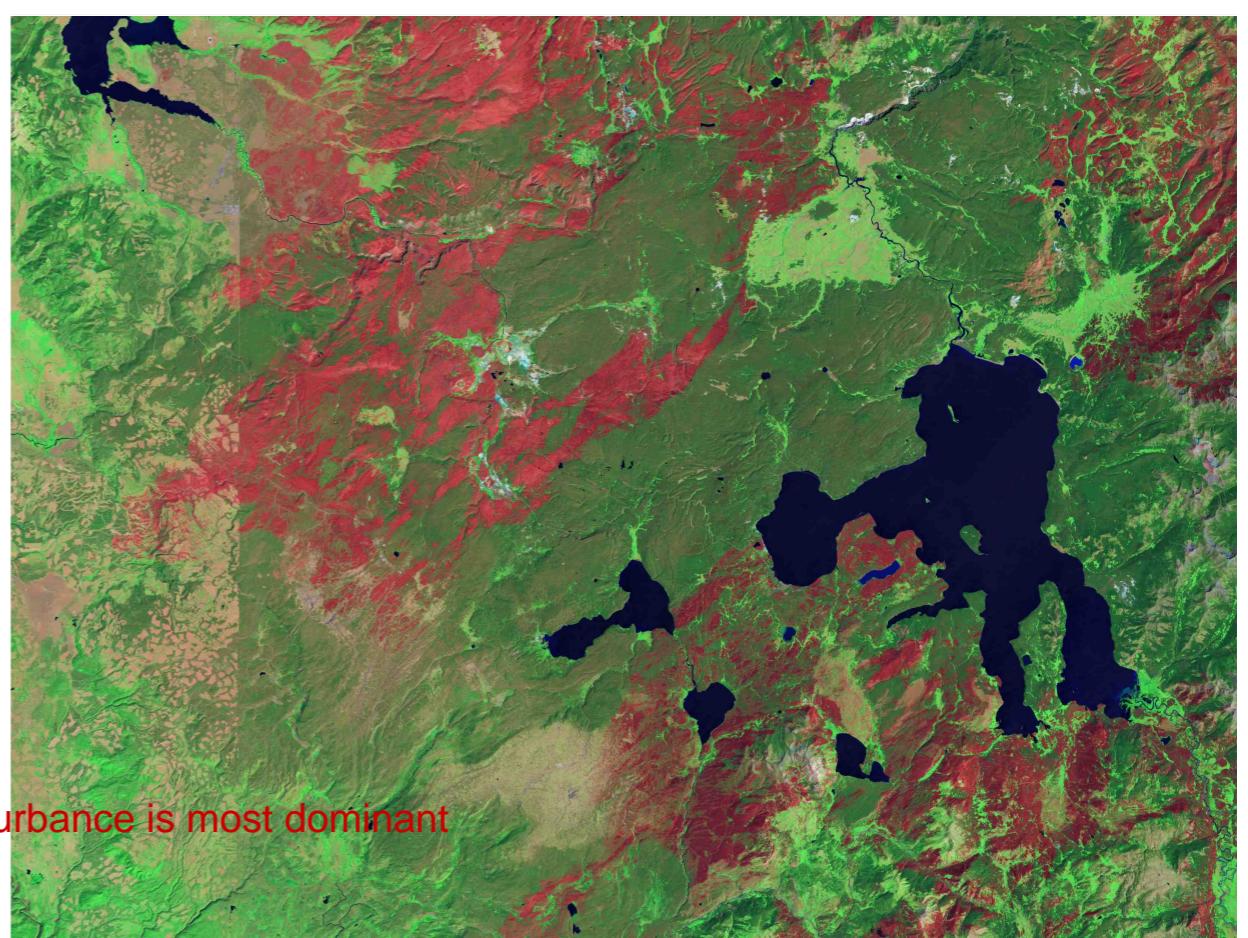


a similar endstate can arise from a different set of processes and vice versa

Agents of spatial pattern - parting thoughts & confounding issues

Inferences regarding the relative importance of the physical template and other factors can be confounded:

- env. gradients are often highly correlated
- biotic responses and disturbance regimes interact with the physical template and each other
- Each factor / process has its own characteristic spatial and temporal scale **characteristic scale is the scale at which the disturbance is most dominant**
- Interpolation often required, but can be extremely challenging in marine environments **and aquatic environments**



Spatial Hierarchy

Local Scale

The most important process at this scale determining vegetation factors: Competition & dispersal (ie. biotic processes)



Landscape Scale



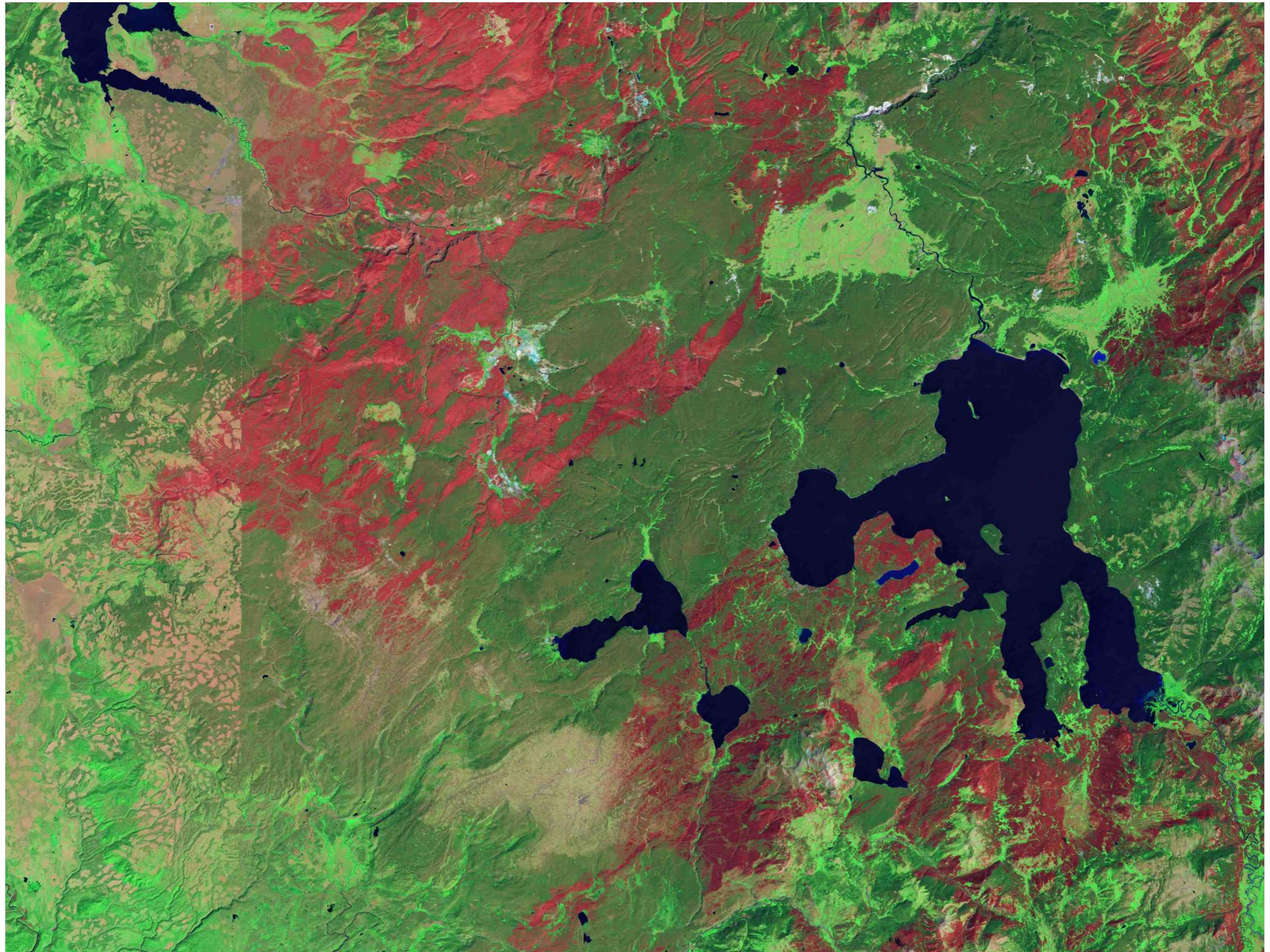
Landscape Scale

landform modifying climate and causing differences in vegetation patterns



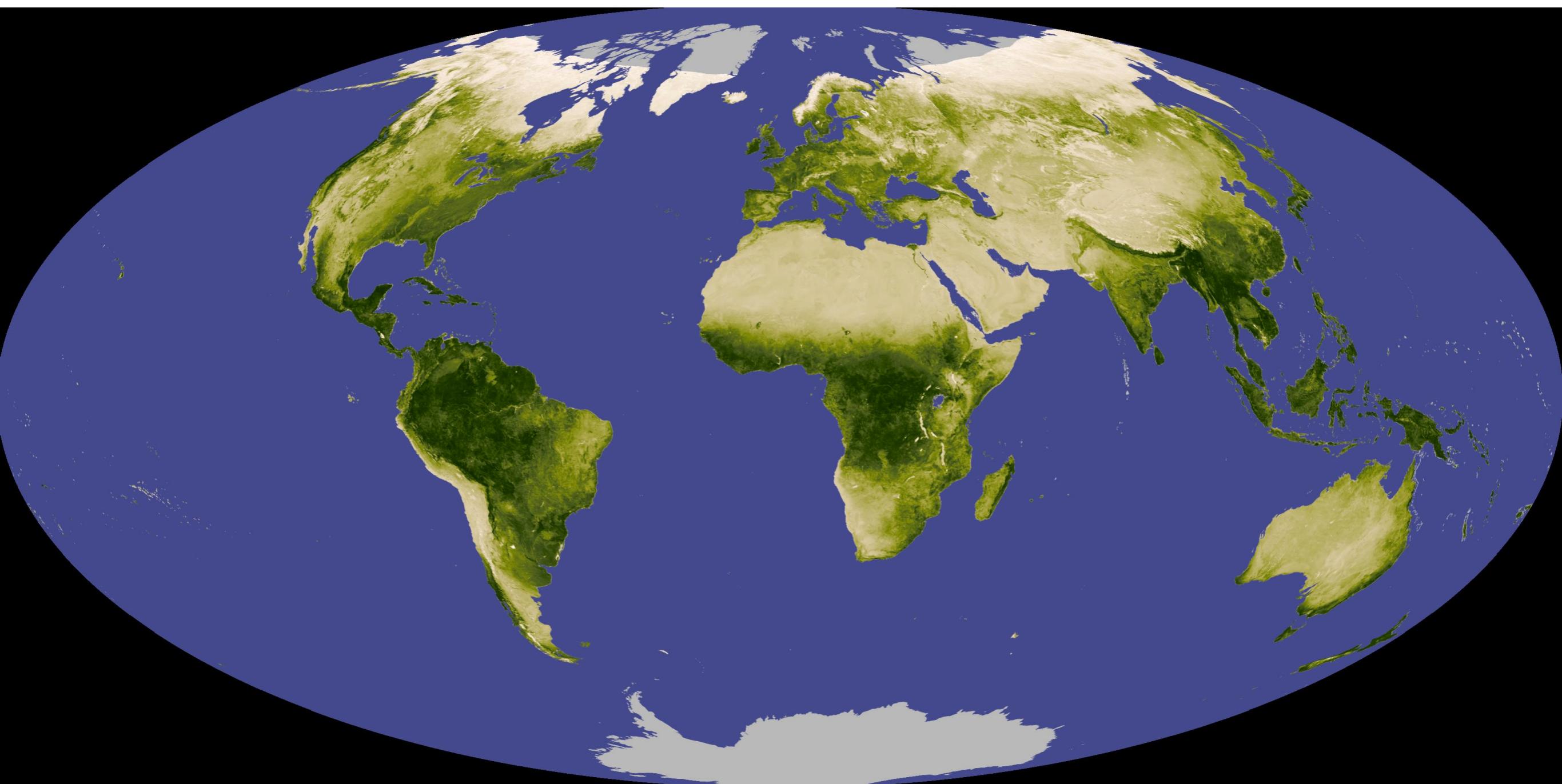
Regional Scale

disturbance and landform effects



Global Scale

climate



Take home points

- Primary agents of landscape pattern: (1) physical template (abiotic environment) is the arena in which (2) biotic processes and (3) disturbance regimes interact.
- Landform (terrain) modifies climate to produce microclimate & variation in water balance
- Historical contingencies & legacies can be critical to understanding current patterns

