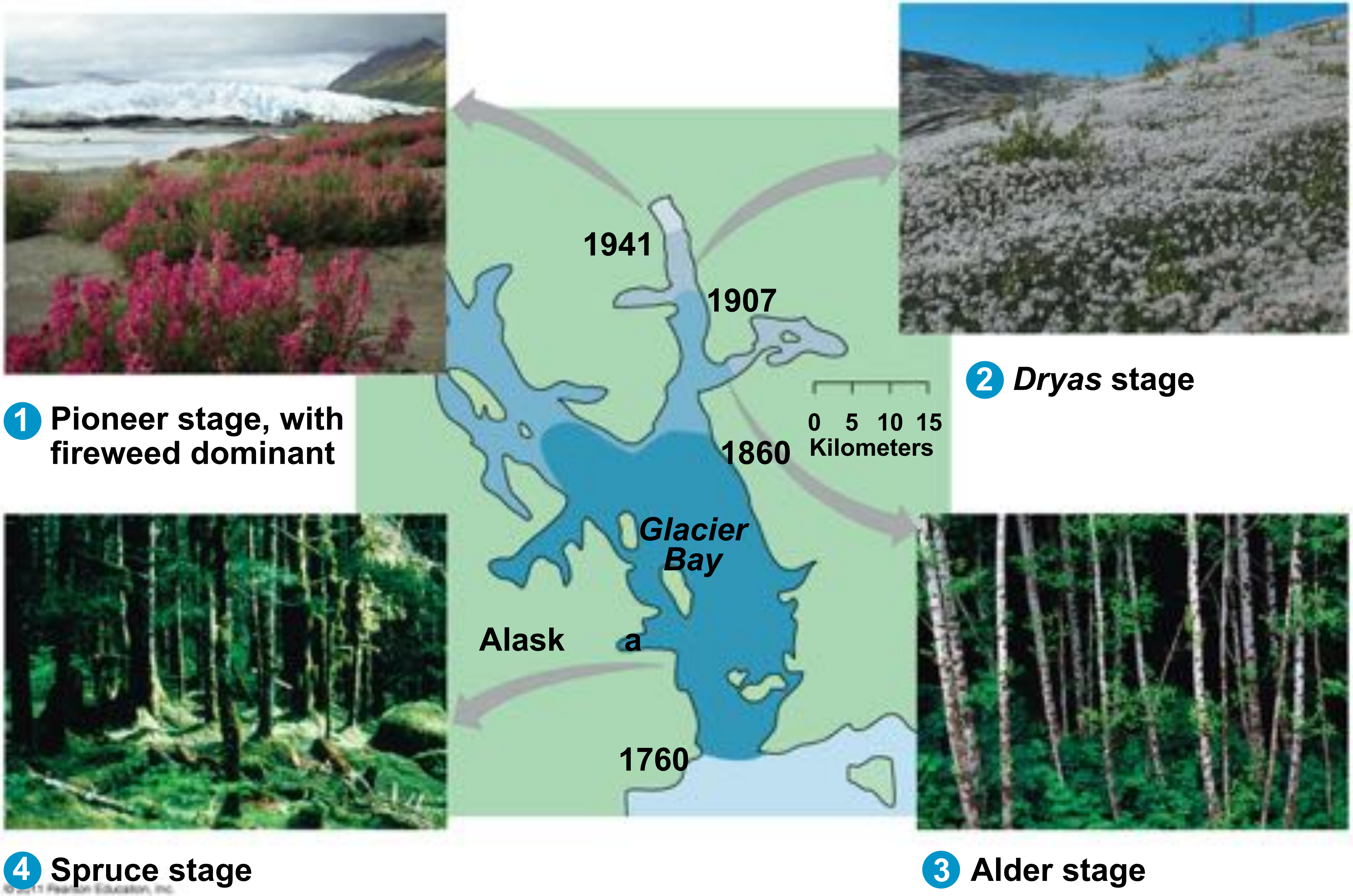
Succession and Community Assembly:

insights from two fields of research

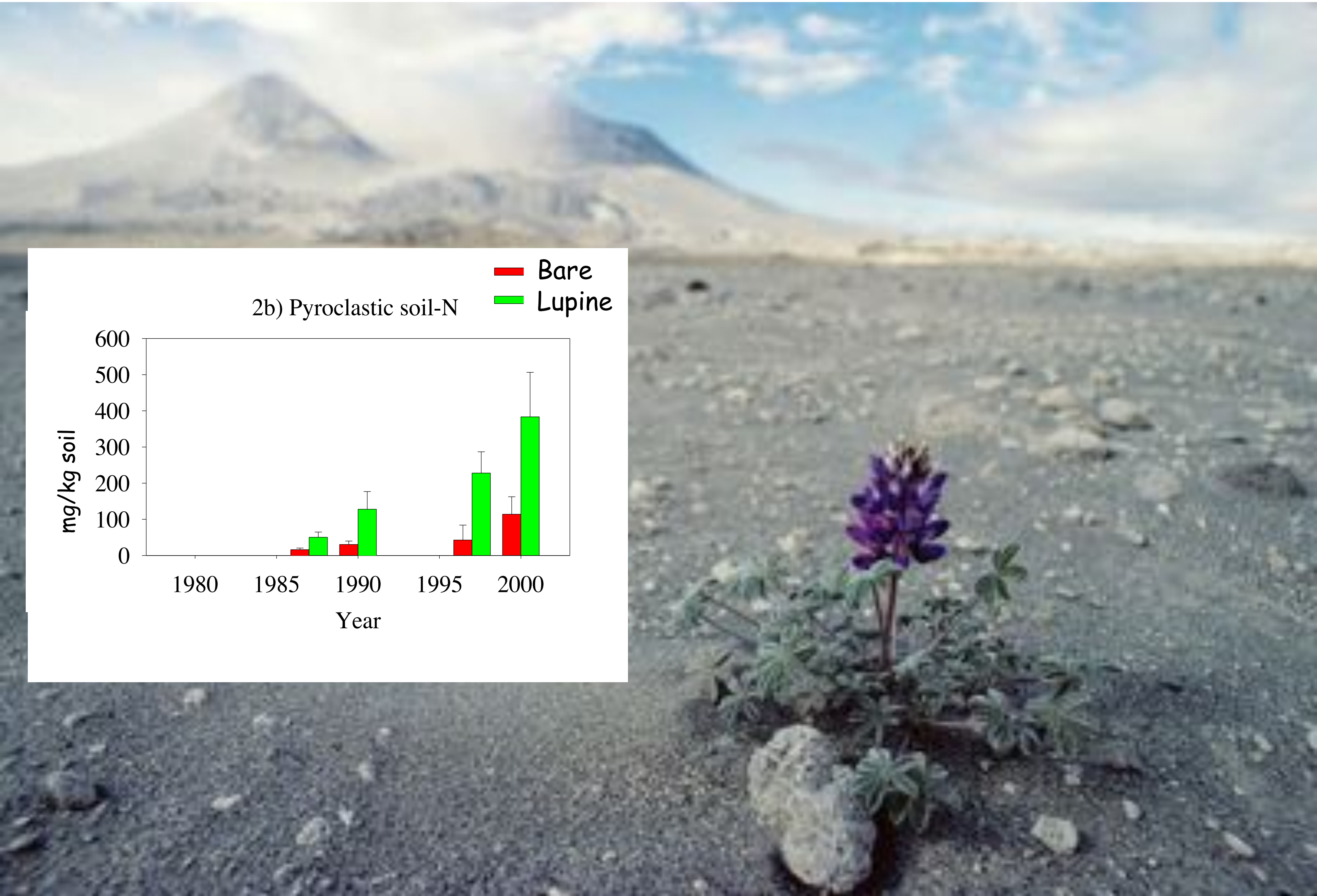
Example 1. Glacial retreat in Glacier Bay, Alaska



Retreat documented since 1760

space = time → chronosequence

Example 2. Eruption of Mt. St. Helens May 18, 1980



Pocket gophers survived underground

Mixed underlying soil with ash

→ Facilitation

= a Biological Legacy

Allen and MacMahon 1988

Example 3. Douglas fir forest clearcuts

Phases
Establishment/initiation
Competitive exclusion
Maturation/diversification
Dynamic climax

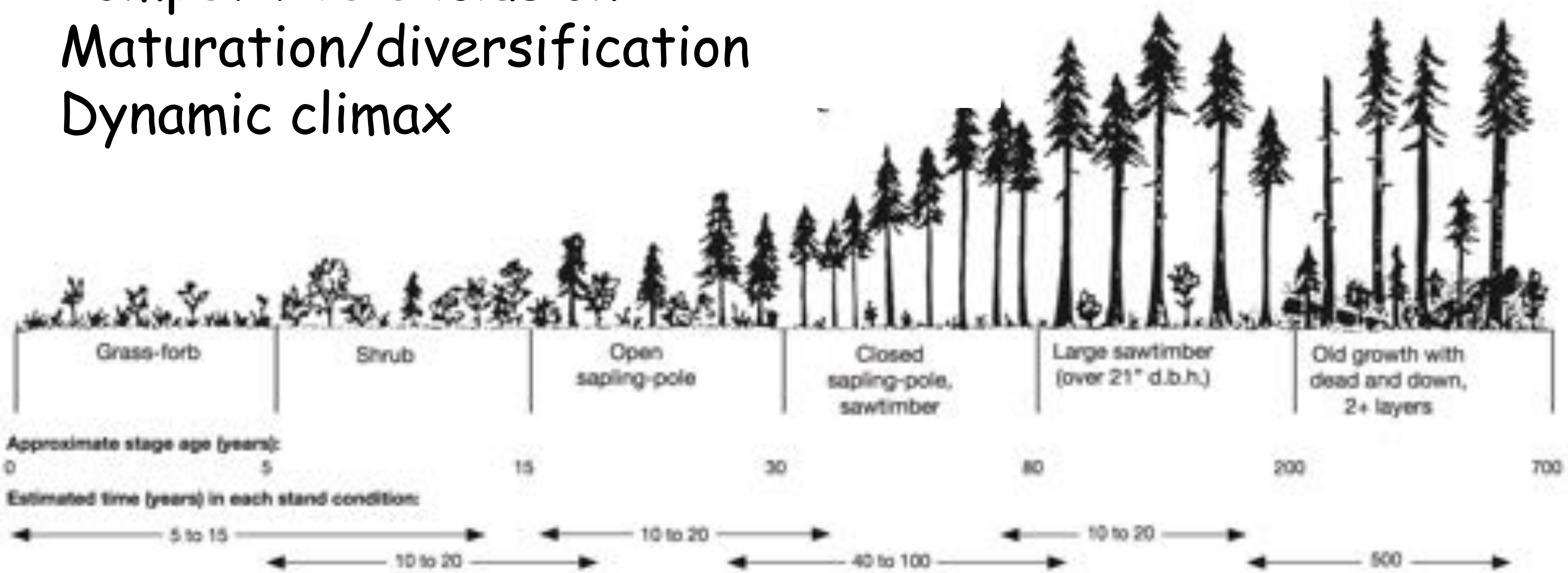


Figure 1. Stand conditions in Douglas-fir forests after even-aged harvesting. ***From Brown (1985).***

Franklin et al. 2002. Forest Ecology & Management 155:399-423

Mechanisms and Models of Succession:

Early ideas: Clements and Gleason

The mechanisms: Connell and Slatyer

The models: Egler, Grime, Tilman,
Westoby and Philips

Clements (1916, 1928)

Communities – as "superorganism"
- each seral stage a discrete entitity

Succession – predictable and orderly
- from a bare state to a climax community
- via series of invasions by "higher forms"

deterministic

"The .. study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies." — Frederic Clements

Gleason (1917, 1926, 1927)

Communities – as a continuum
- intergrade

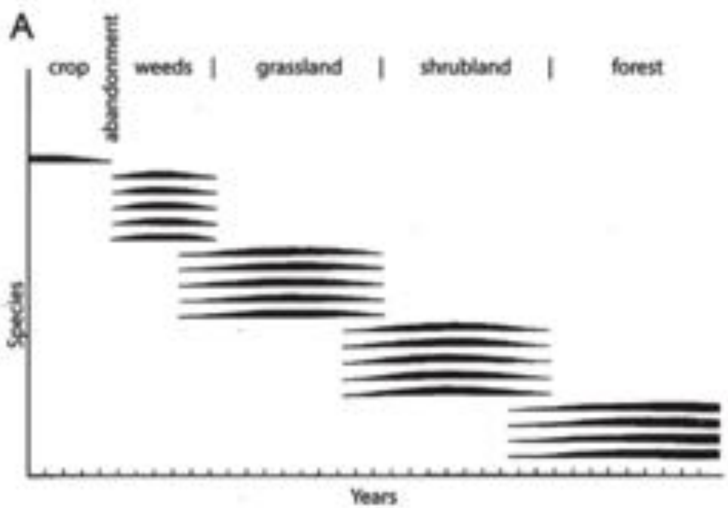
Succession – a continuous process with no end point
- linked to plant traits
- those least tolerant of changing environment drop out
- chance colonization events are important

contingent

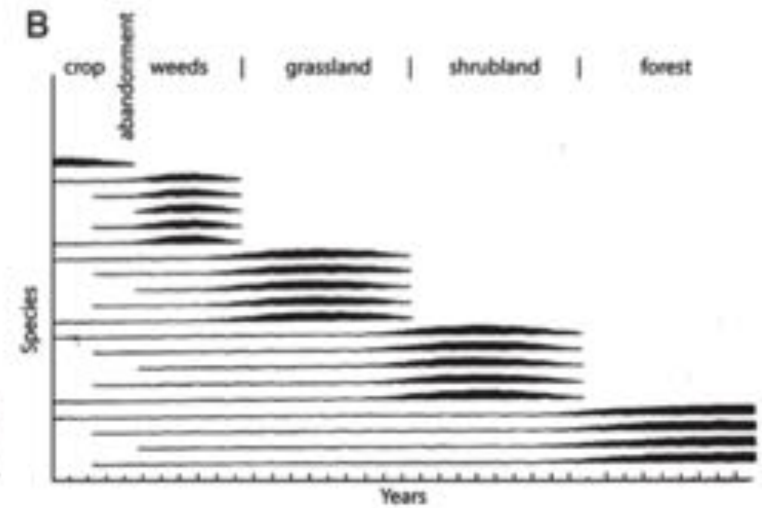
"An association is not an organism, scarcely even a vegetational unit, but merely a coincidence."
— Henry Gleason

Egler (1954) – two models

Relay floristics



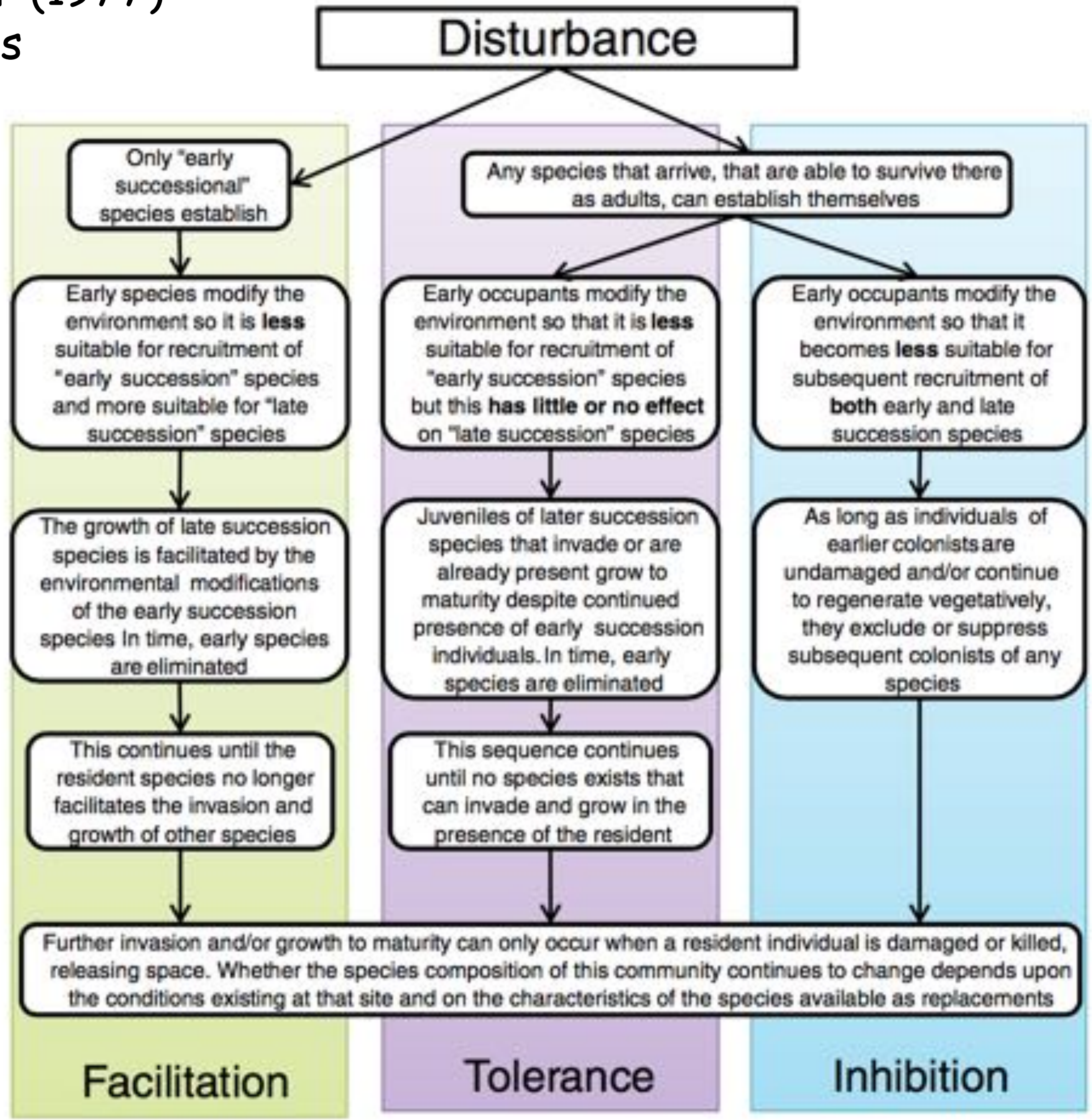
Initial floristic composition



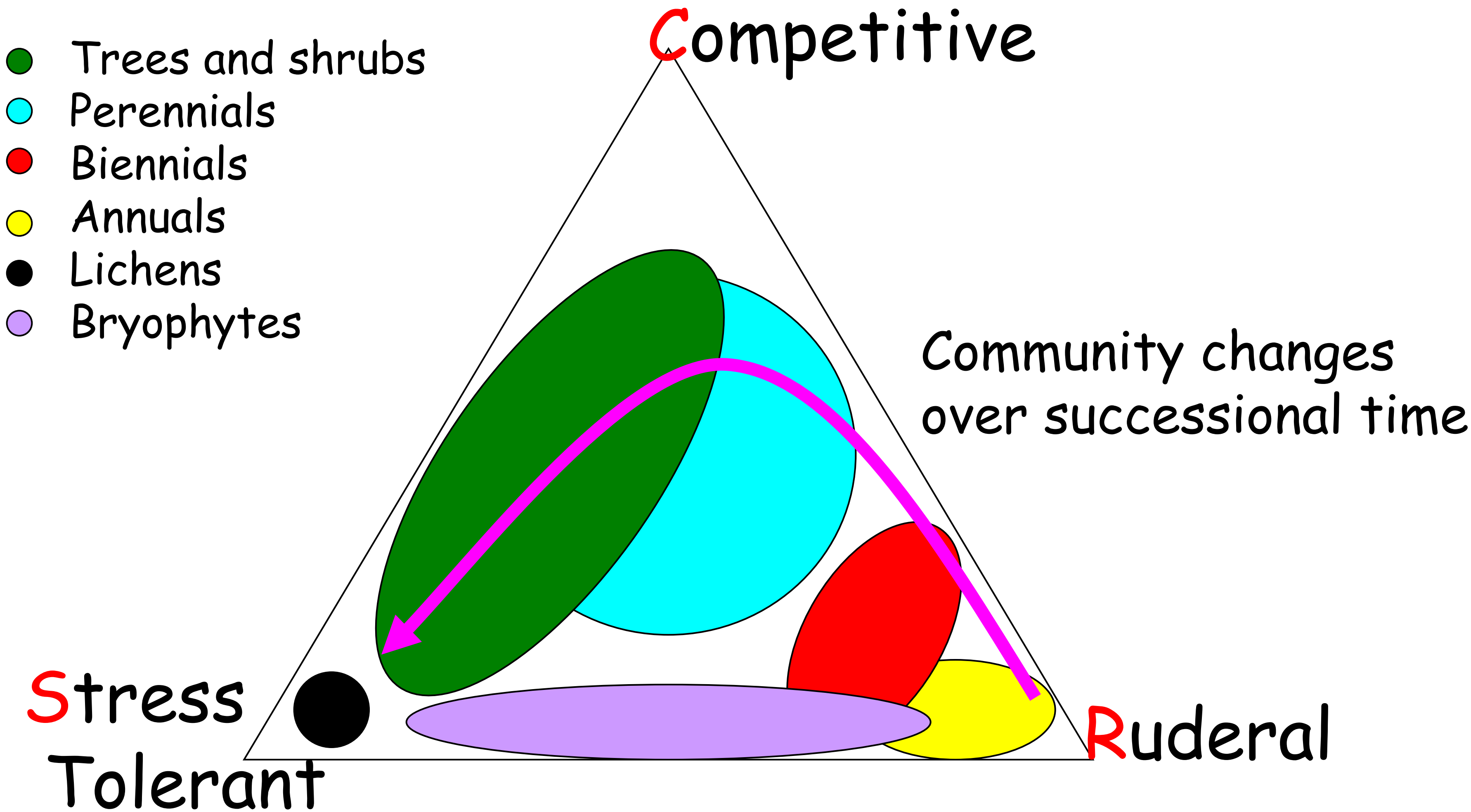
Emphasis – facilitation

initial colonization

Connell and Slatyer (1977)
- three mechanisms



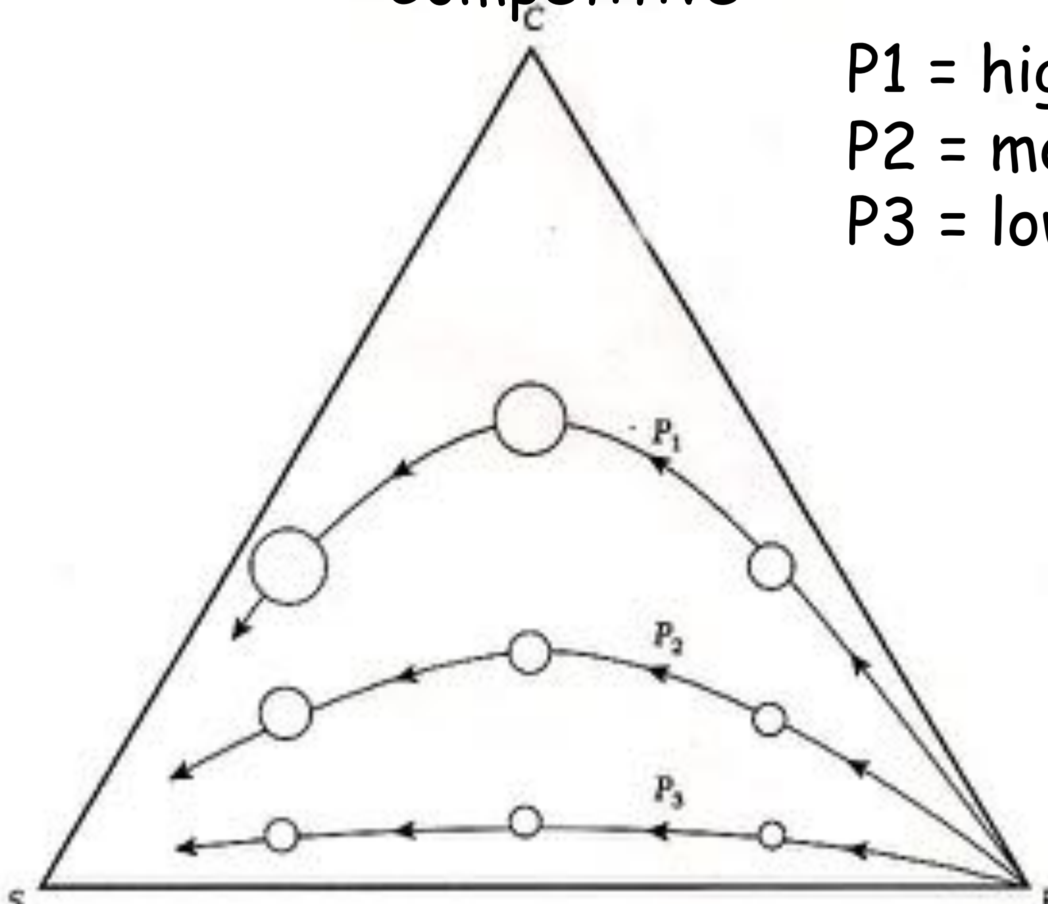
Grime (1977, 1979)



Grime (1977, 1979)

Competitive

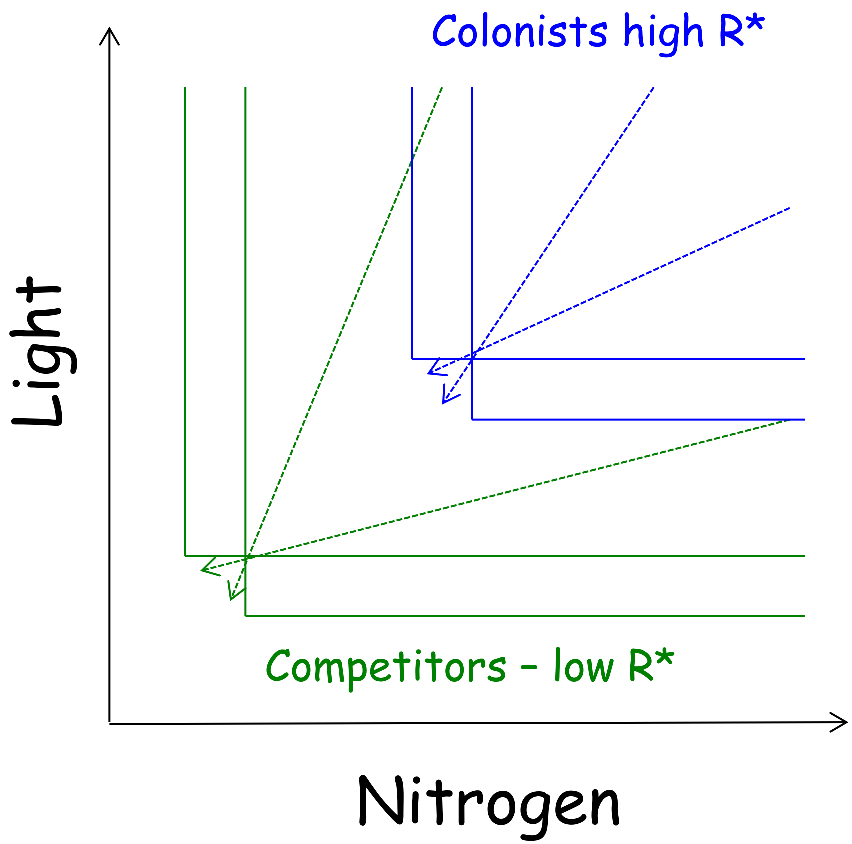
P1 = high productivity
P2 = moderate
P3 = low



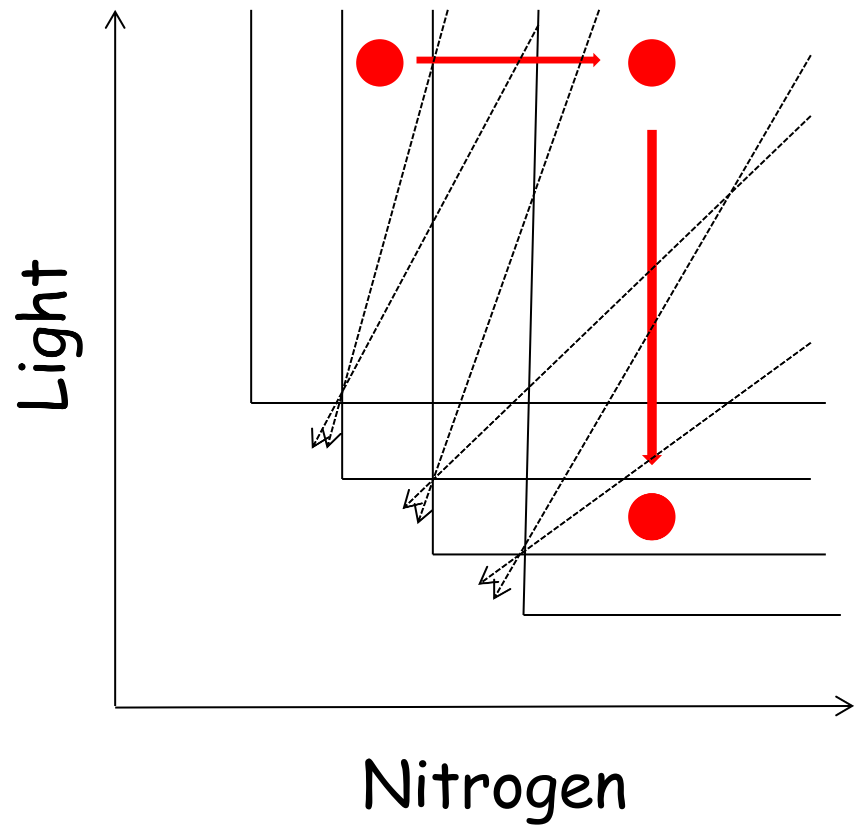
Stress tolerant

Ruderal

Tilman (1985, 1988) Resource-ratio theory



Succession- outcome of a
Competition-colonisation trade-off



Facilitation and shade alter the
resource supply points and
outcome of competition

Westoby et al. (1989), Phillips (2011)

State and transition models

Multiple states are possible

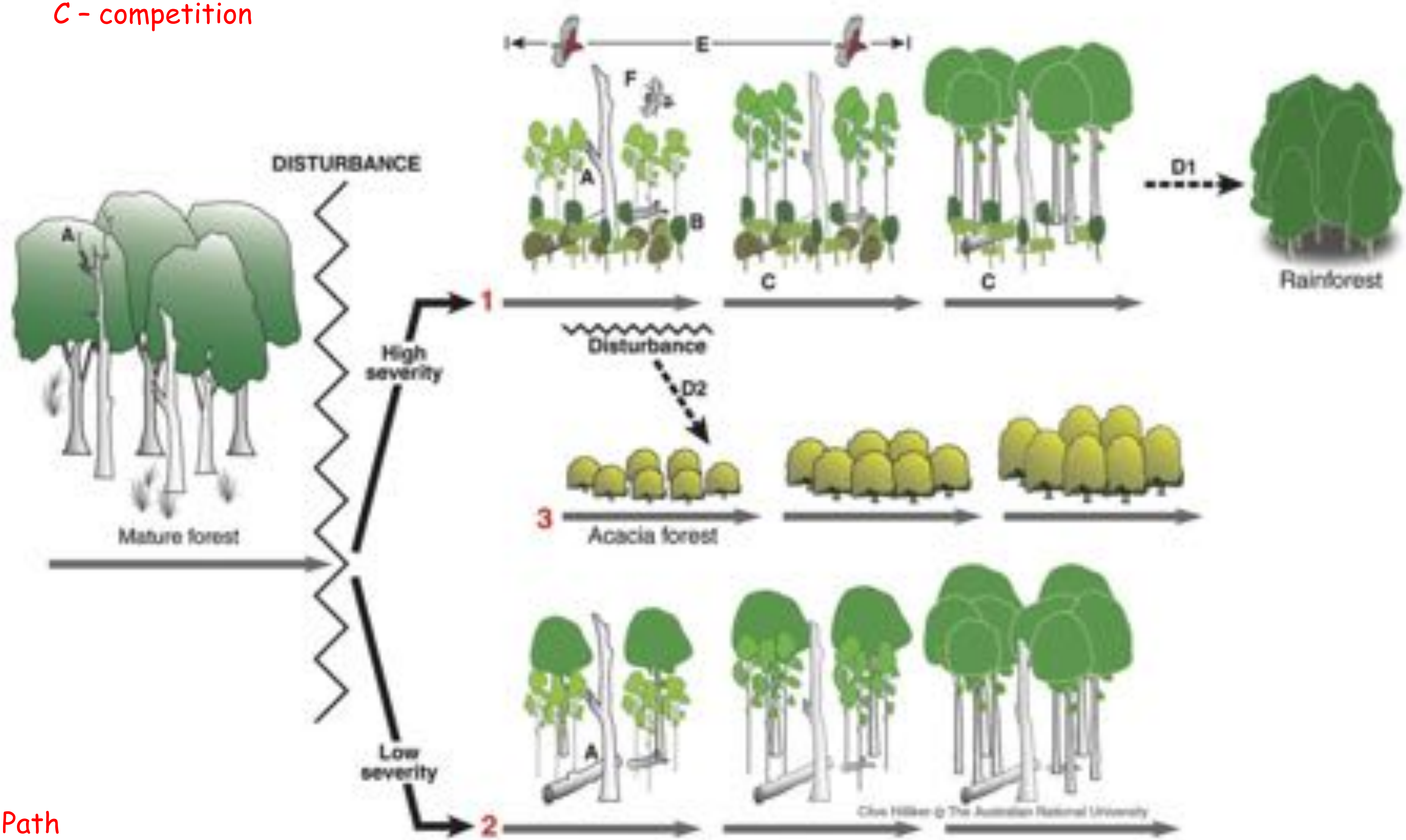
Transitions

- gradual or abrupt
- natural or anthropogenic
- multi-directional

Emphasis - "drivers" of transitions

A -biological legacy –dead logs/trees
B- initial floristic composition
C – competition

D - state transitions
E – habitat accommodation model
F – trait-based presence/absence



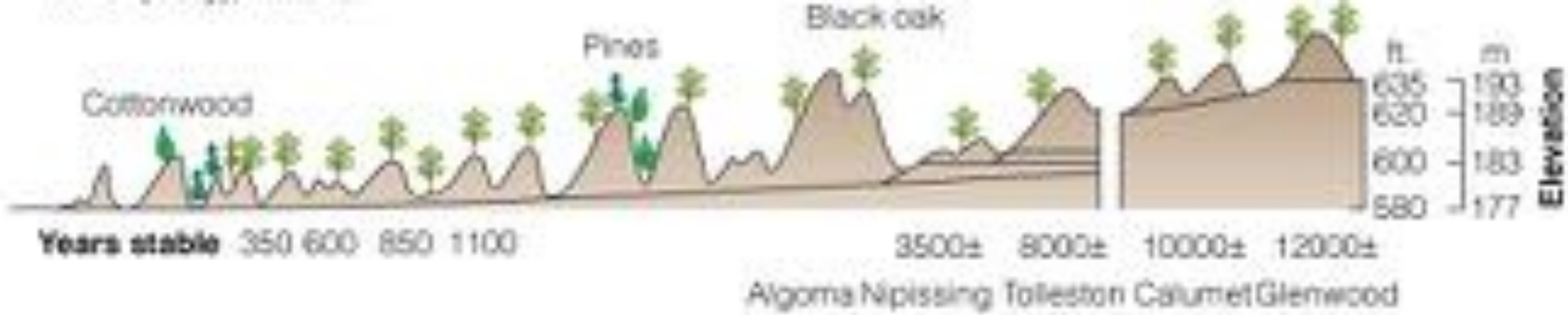
Path
1.- main pathway – infrequent stand replacing fire
2. - low severity fire
3.- stand replacing fire in young stand → transition

Central Questions in Studies of (Plant) Succession

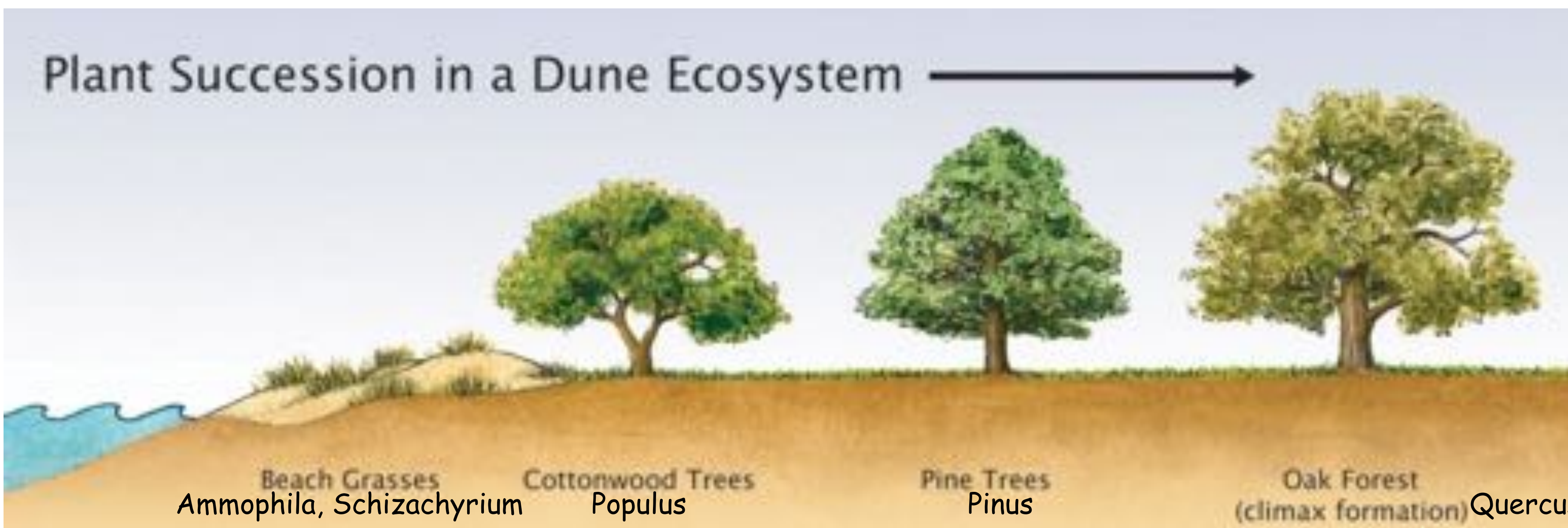
How predictable is succession?

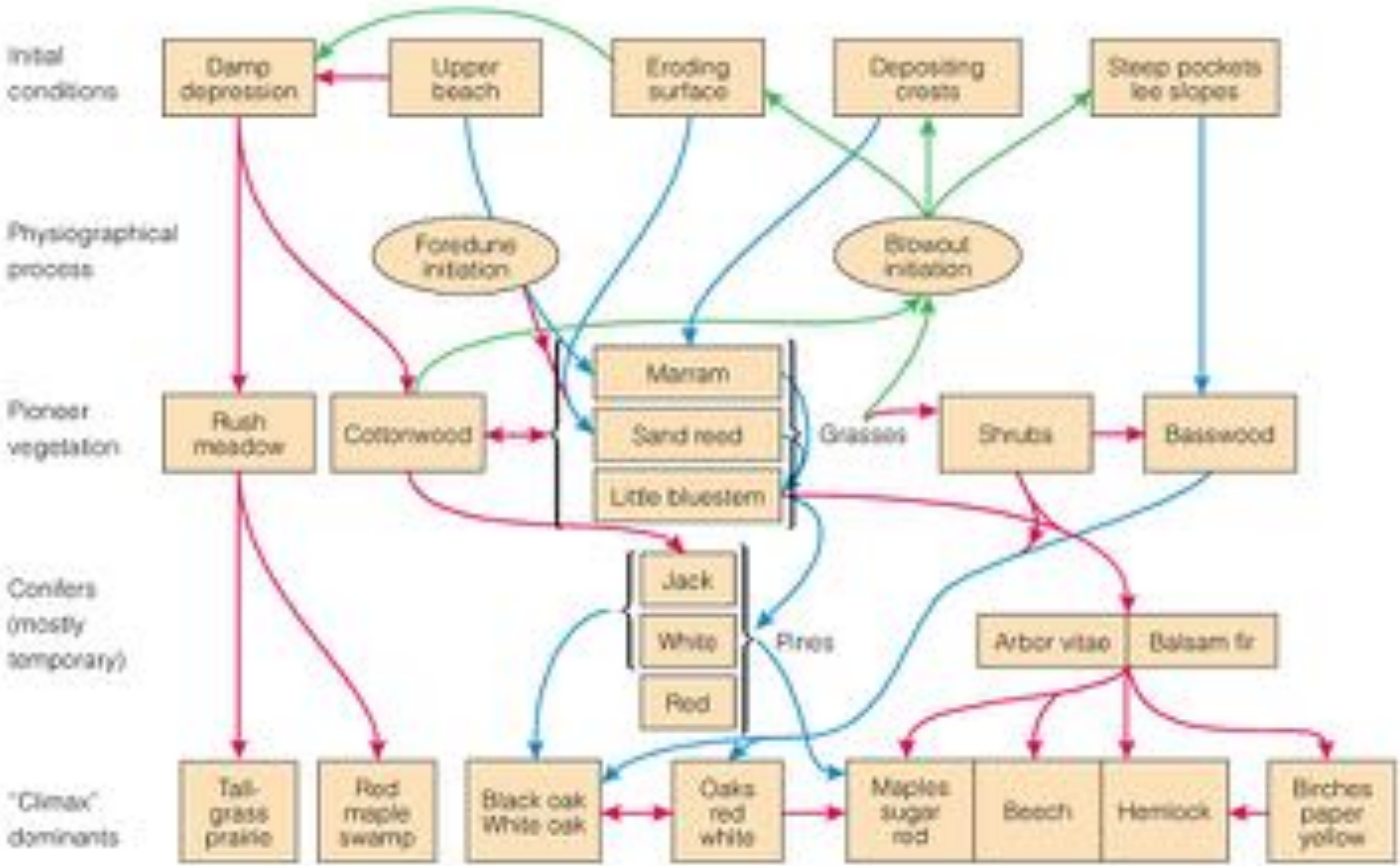
Does succession produce a climax community?

What mechanisms/processes are operating during succession?



Henry Cowles
1899
Jerry Olson
1958
Lake Michigan
Sand Dune
Succession





Blue lines indicate most common successional path

The climax state

"final seral stage or stable state in a successional series"

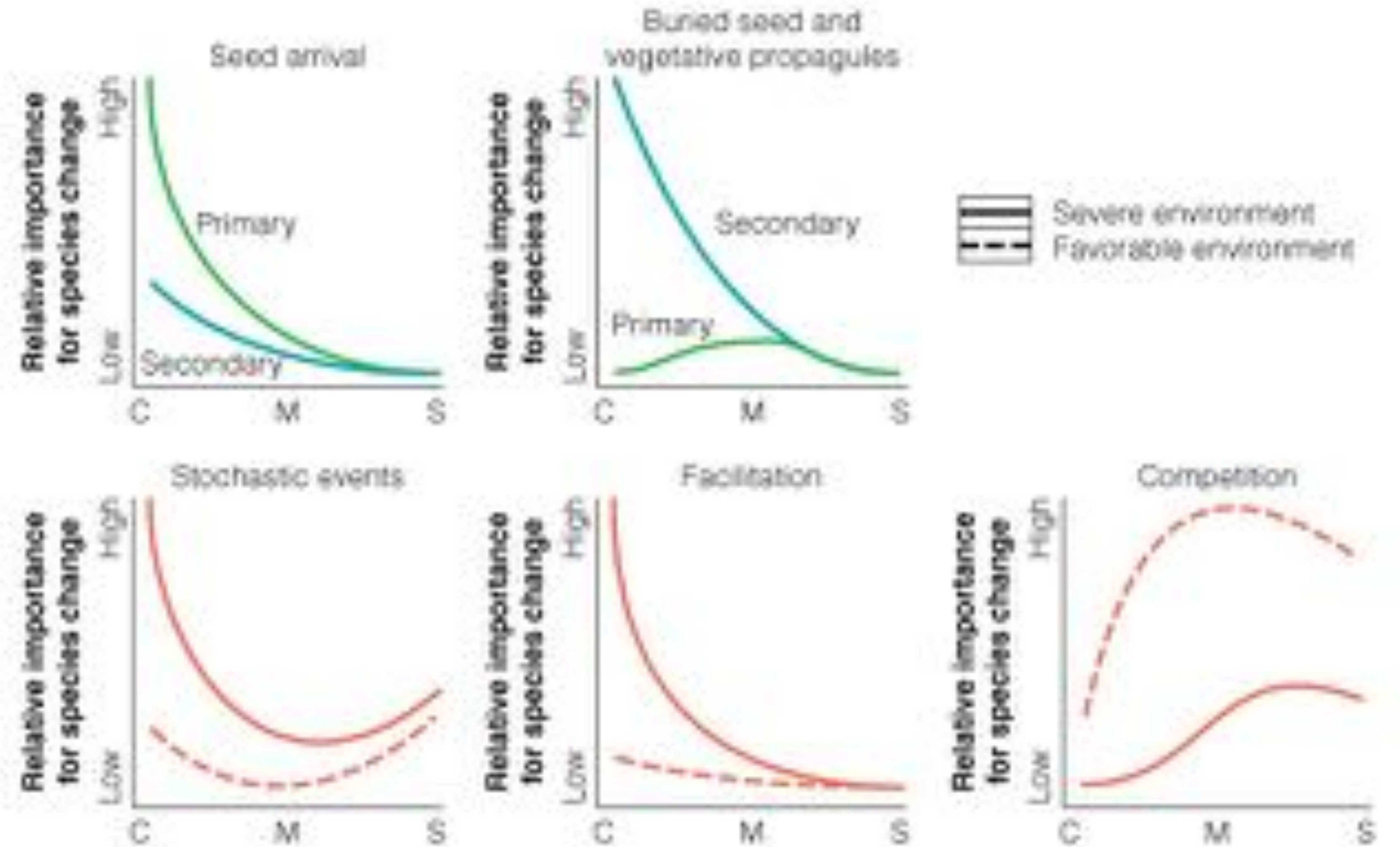
Monoclimax – Clements 1916
Polyclimax – Tansley 1939
Climax –pattern – Whittaker 1953 – continuum of climax types

" in equilibrium with the physical and biotic environment"

but climate and biotic environment is variable
succession can be very slow

Subalpine forest, Cypress – 2000 yrs post-fire
– community still undergoing successional change

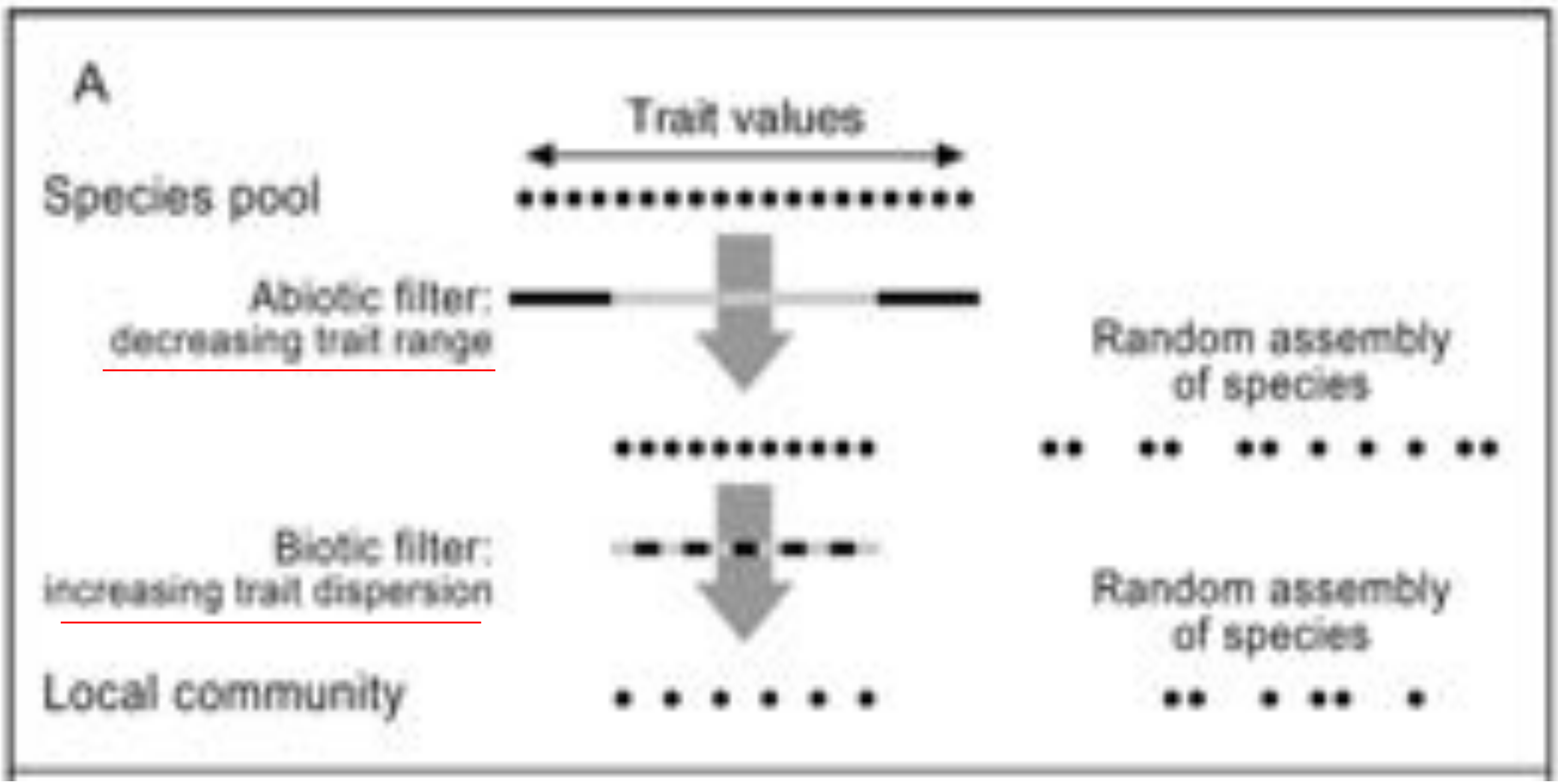
Importance of different processes during succession



C – colonization, M – maturation, S – senescence=late

Community assembly

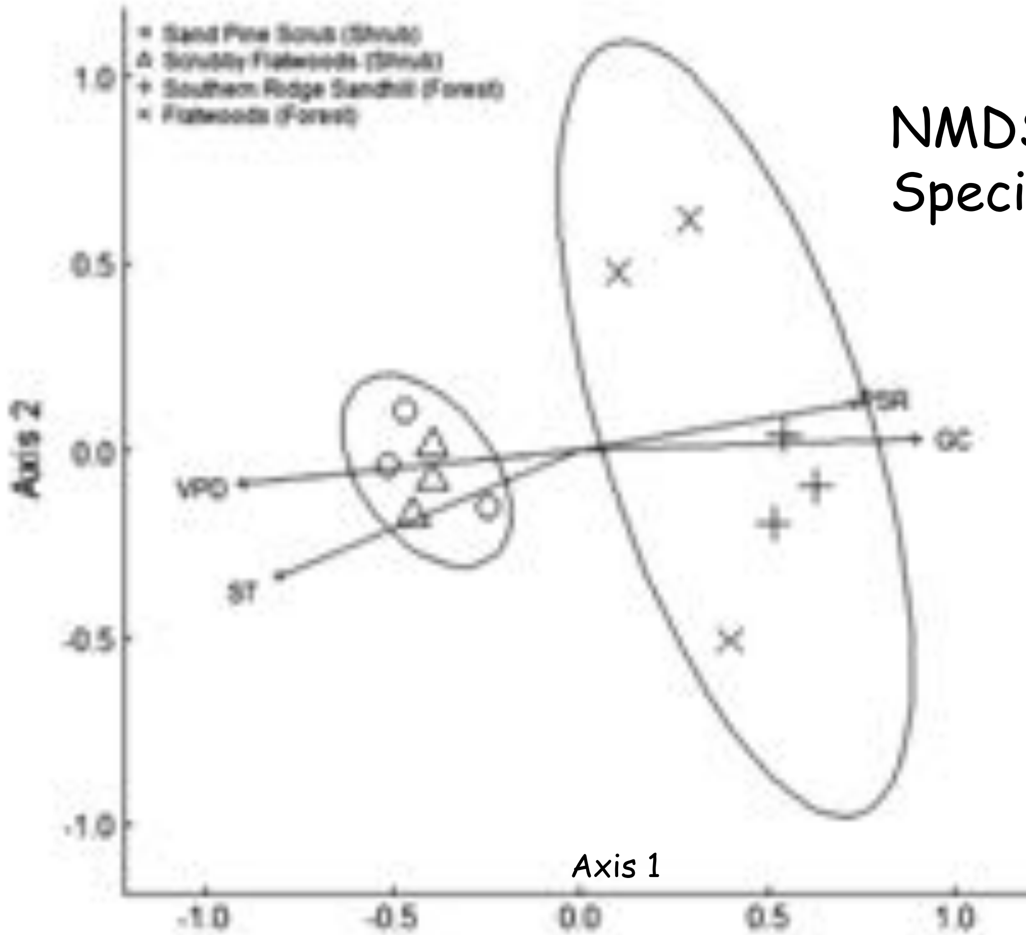
Community assembly



Abiotic filters

Ants – Archbold Biological Station, Florida
4 habitats, 19,000 ants   37 spp

Surface temp, Vapor pressure deficit
Ground cover, species richness



NMDS plot
Species space

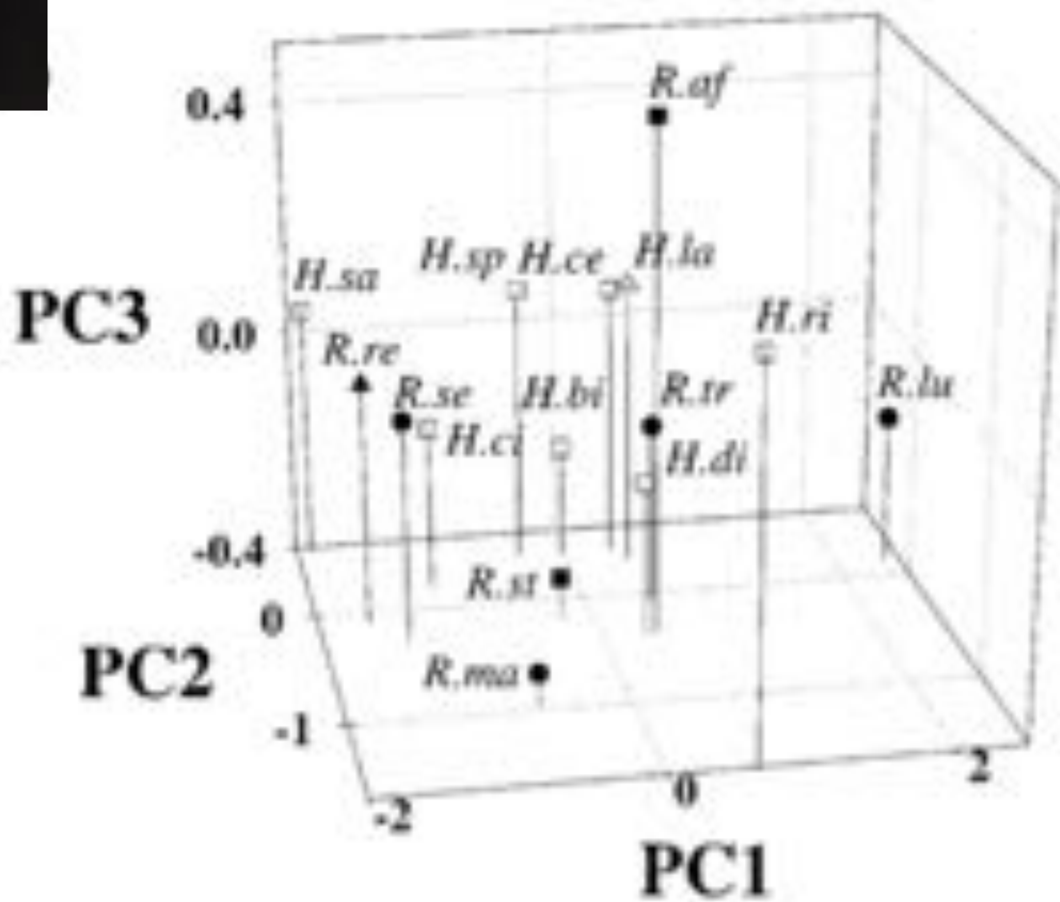
Abiotic filters

Ants – Archbold Biological Station, Florida
4 habitats, 19,000 ants   37 spp

Table 3 Modified fourth-corner analysis of the correlations between species traits and environmental variables for all and common species

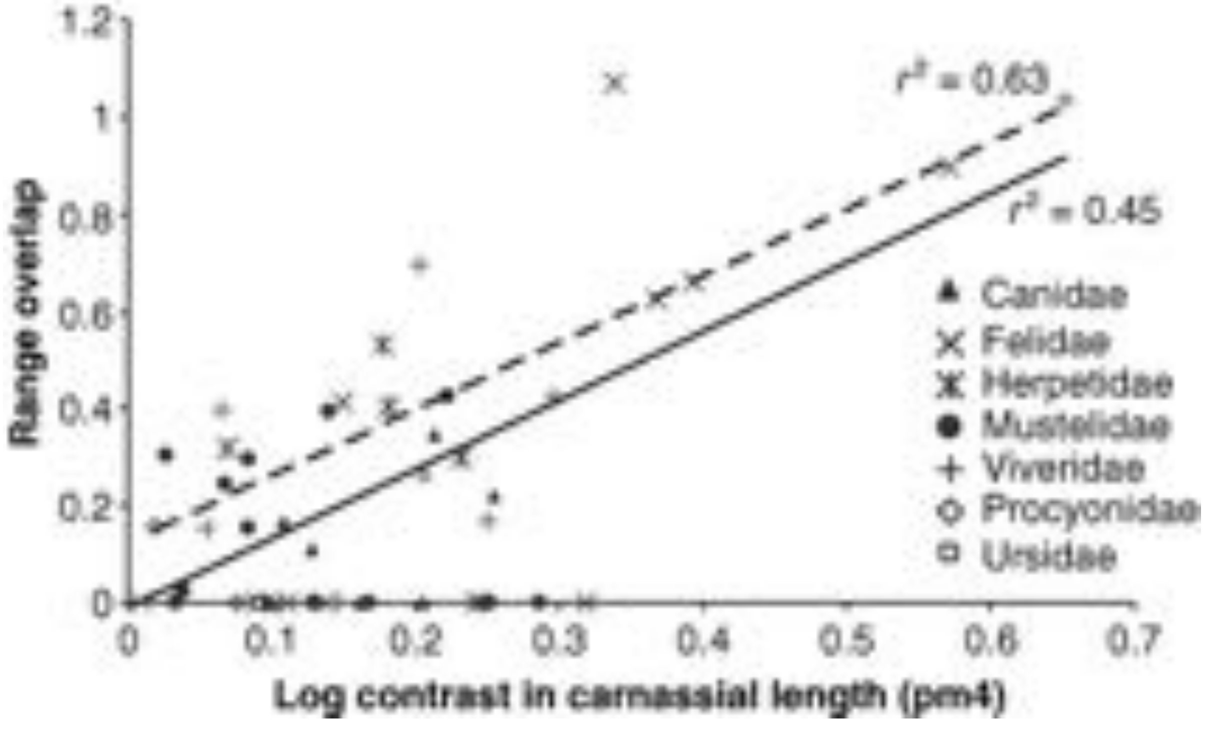
Trait	Groundcover (%)	Surface temperature (°C)	VPD (kPa)
Common species dataset			
Mass (mg)	0.049	−0.063	−0.028
HW (mm)	0.061	−0.072	−0.040
HL (mm)	0.071	−0.080	−0.047
LL (mm)	0.056	−0.061	−0.026
RL	**−0.186**	**0.189**	**0.176**
FTL (°C)	**−0.147**	**0.134**	**0.150**
LT (°C)	**−0.208**	**0.184**	**0.214**
AIWLR ($mg \times h^{-1} \times cm^{-2}$)	−0.005	0.004	0.016

Trait overdispersion in rhinolophoid bats



PC1 – size
PC2 – call freq
PC3 – wing area

Character divergence and range overlap in Carnivora

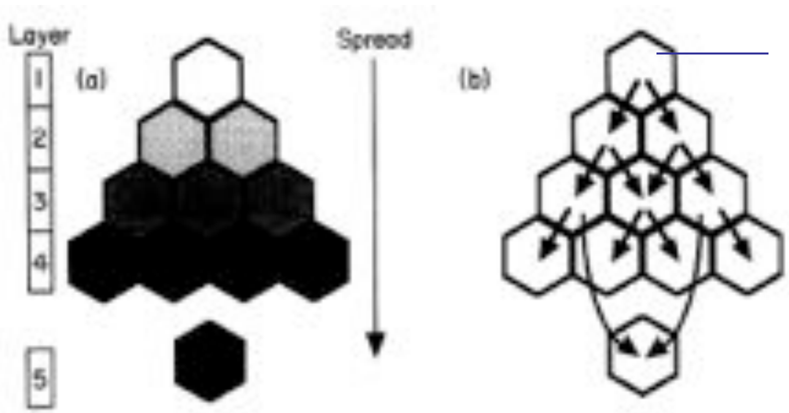


Davies et al. 2007 Ecology Letters 10:146-152

Community composition

Chance events during assembly

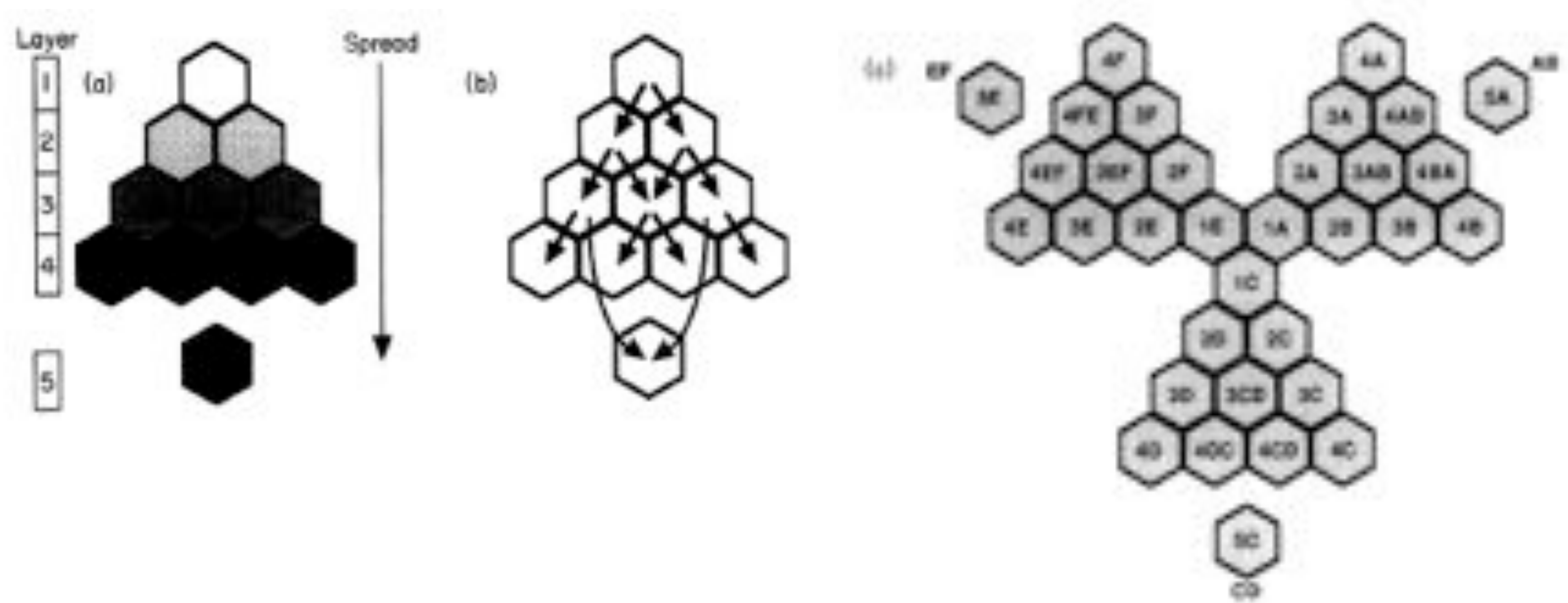
Drake et al. 1993 J Anim Ecol 62: 117-130



1litre bucket = mesocosm

Species pool
4 planktonic algal spp
4 inverts - 2 Cladocera - filter feeders
- 1 Ostracod - settled plankton/detritus
- 1 Copepoda - suspended particles or act as predator

Community composition – chance events



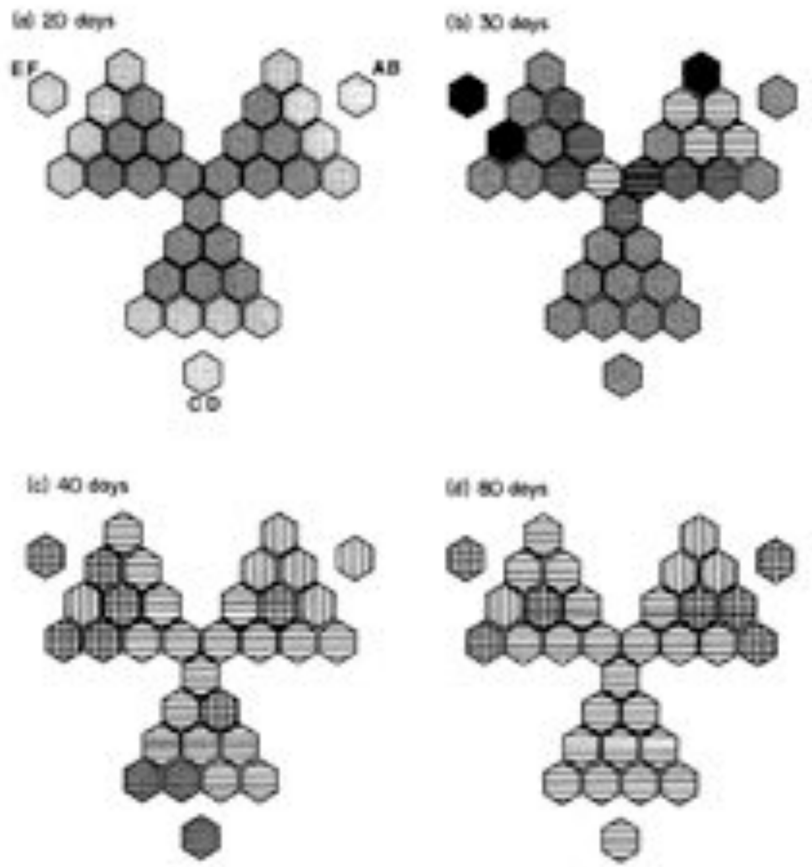
Each 5 day interval

add 1 spp to layer 1

transfer random sample to next layer

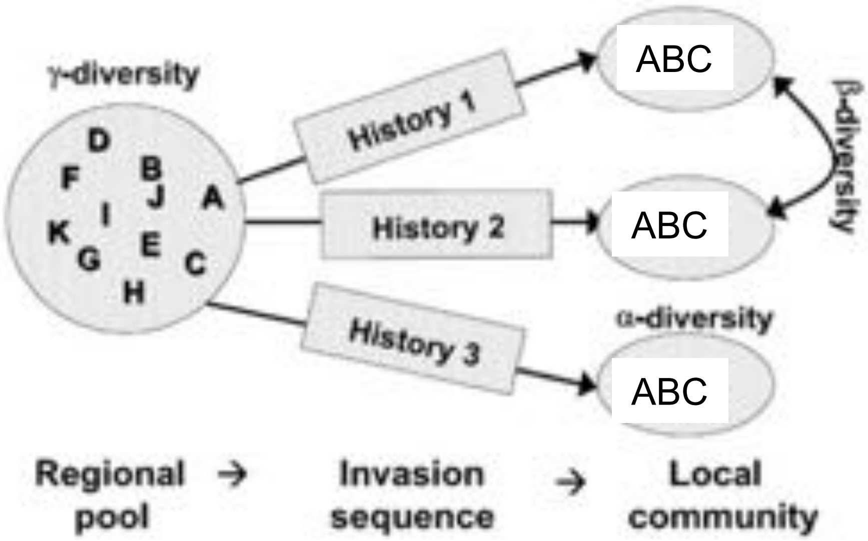
3 replicates - identical invasion sequence

Community assembly – Chance events

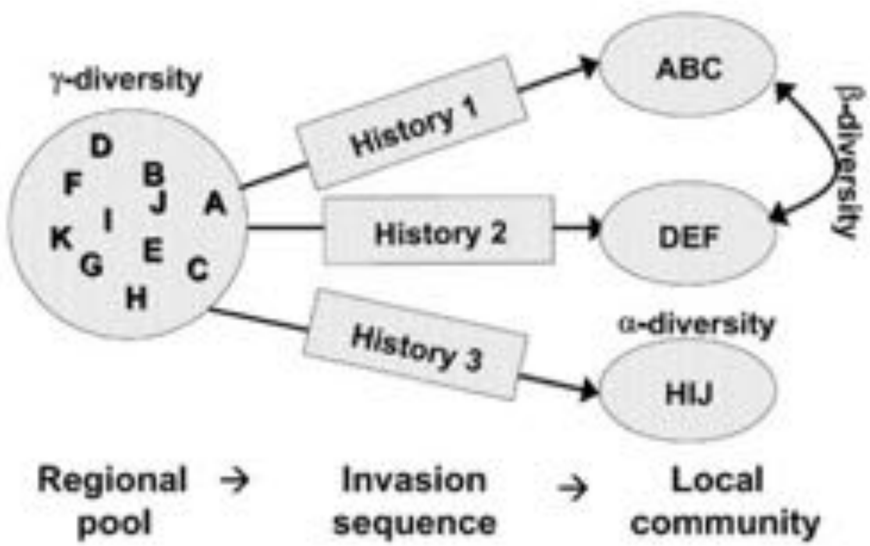


Differences in invasion success and persistence --> alternative stable states

Different pattern = different community



History varies but one single stable state



History varies → multiple stable states

Chase 2003 Community assembly: when should history matter?

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Predictions regarding dissimilarity = beta diversity

1 Size of the regional pool

2 Rate of dispersal / connectedness

3 Primary productivity

4 Disturbance

Chase 2003 Community assembly: when should history matter?

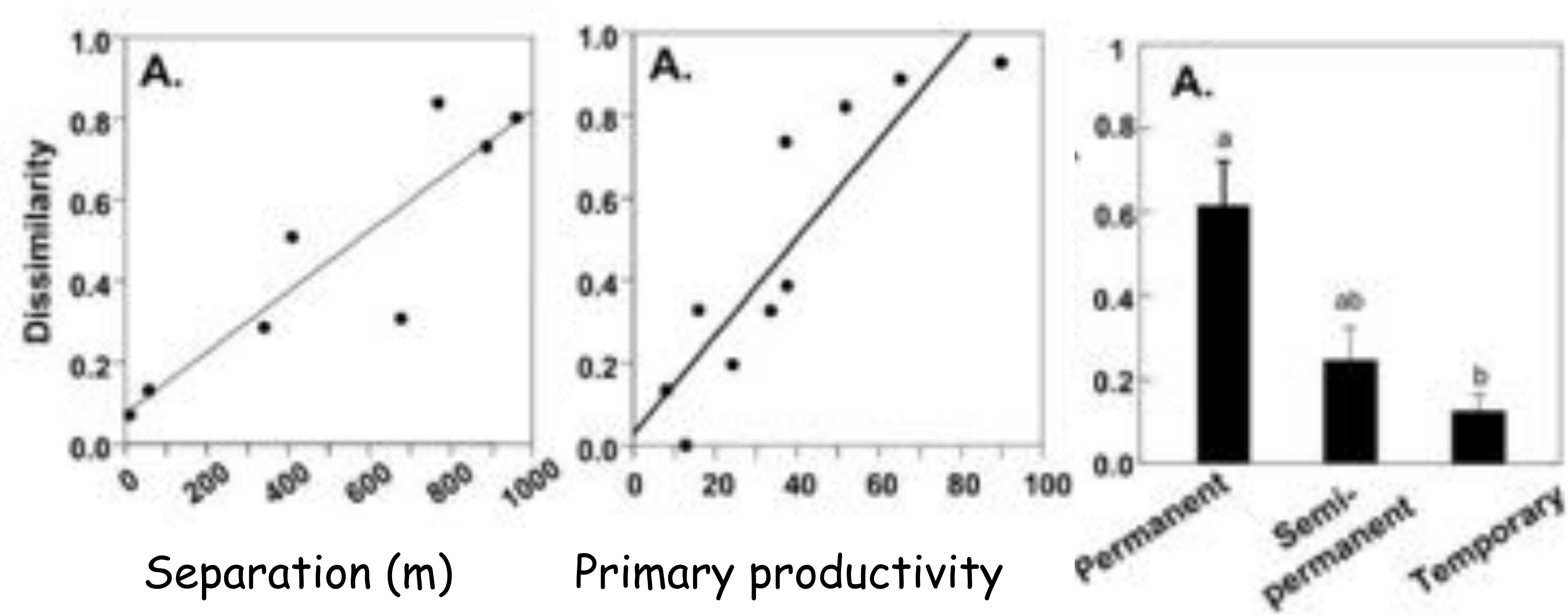
Empirical tests in 72 ponds

Benthic inverts
Benthic and free-swimming insects
Amphibians
Small fish

local scale = pond (alpha diversity)
regional scale = three local ponds in watershed (gamma)

Inter-pond dissimilarity – 1 no species shared
- 0 all species shared

Chase 2003 Community assembly: when should history matter?



Conclusions from Study of Community Assembly

Abiotic factors determine the pool

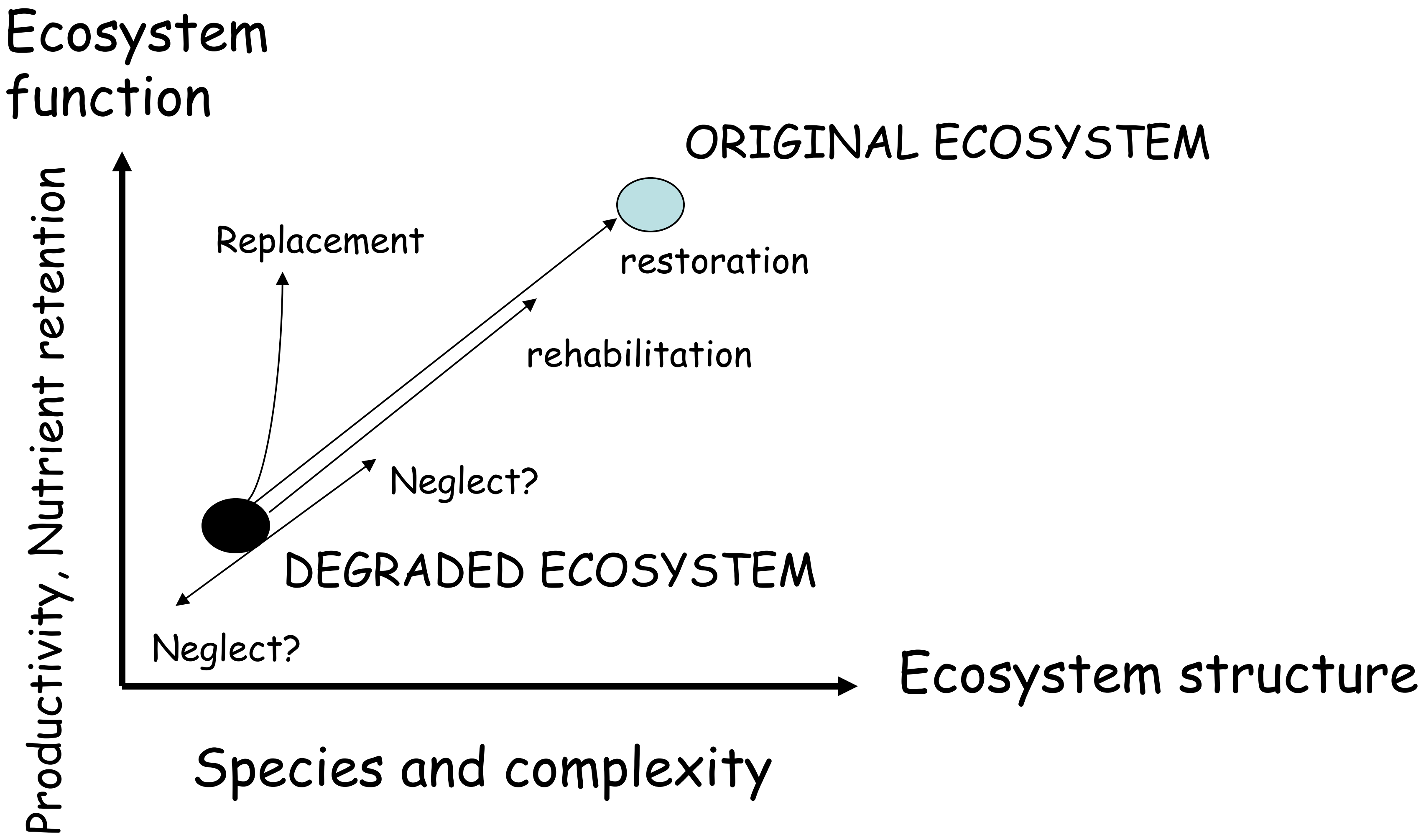
Assembly rules may determine potential subsets

Assembly rules have limited ability to predict communities

History (sequence and chance effects) can influence the community

History is more important when the species pool is large, dispersal is high, primary productivity is high, disturbance is low

RE-ASSEMBLING COMMUNITIES
Restoration and recovery of function/structure



Restoration

What does theory suggest about
- restoring function
- restoring specific communities

How effective have restoration efforts been?

Restoration of ecosystem function

Ecosystem function is related to species diversity
Ecosystem functions are achieved with a large number of spp combinations

But not all species are required

SO - Restoration of function should be feasible

Restoration of ecosystem structure

Theory

Secondary succession – historical view
community composition moves along a traditional pathway to a pre-determined endpoint
→Restoration may be accomplished using natural processes

Community assembly - theory and experiments
the final community is often dependent on invasion sequence
→Restoration should manage sequence

Alternative stable states
perturbations may push a community into an alternative state that is stable and hard to return to the original state

Restoration and ecosystem structure

Overall, theory suggests

1) Natural process may not lead to recovery

2) The degraded community may be stable and resist recovery

3) if the abiotic environment is completely restored
   the restored community may not be a carbon copy of the original community because
      the invasion sequence and chance events influence the outcome

WHEN DOES RESTORATION SUCCEED?

Lockwood and Pimm 2004
87 projects - attempt to restore native ecosystem

Classified goals -
- function- eg water quality, erosion control, productivity
- partial structure - some native diversity restored
- complete structure - previous community re-established

Variables - Duration 1-53 years
- System Freshwater, marine, terrestrial, wetland
- Size 1-10 ha, 11-50 ha, > 50 ha

WHEN DOES RESTORATION SUCCEED?

Lockwood and Pimm 2004
87 projects - attempt to restore native ecosystem

Function	Success %	N
Water quality	92	12
Erosion	75	12
Productivity	38	34
Sustaining habitat	73	22
Structure		
Partial	46	70
Complete	6	34

Lockwood and Pimm 2004

Theory suggests

restoration of function should be far easier than reconstructing communities

restored communities are unlikely to be exactly the same as pre-disturbance communities even if abiotic conditions are identical

Restoration projects

May restore function more successfully than structure

Partial restoration is more likely than complete restoration

Ability to restore previous community varies across taxonomic groups

REHABILITATE

Eg. Fresh Kills Landfill, NY City

- Received urban waste for 50 yrs
- Created four mounds 40m tall
- Mounds "capped" 2001-2011

Goal

Restore wetlands, grasslands and woodlands that will offer wildlife habitat and natural open spaces

Rehabilitation of Fresh Kills Landfill, NY City

Natural succession
---> little structure, diversity

Manage: planted shrubs, oak, pine, (17 spp)
---> arrival 20 new spp. in 2 yrs

Planting added spp, provided habitat that allowed arrival animal-dispersed seeds

Fresh Kills – North Mound 1997 and 2015

Current research

Can plantings of early-successional species (willow/poplar) speed up canopy closure and progression to forest?

- selection of genotypes adapted to colonizing disturbed habitat with strong growth under ozone levels from urban areas

Evaluating the "field of dreams" model

- if you build it (grasslands) they will come (grassland birds)
- winter surveys (Christmas Bird Counts
- summer surveys

Biodiversity and filtering of pollutants in tidal wetlands

Peat Extraction in New Zealand

Options

Processed peat islands 5 m diam

Processed peat islands 5m diam + seed

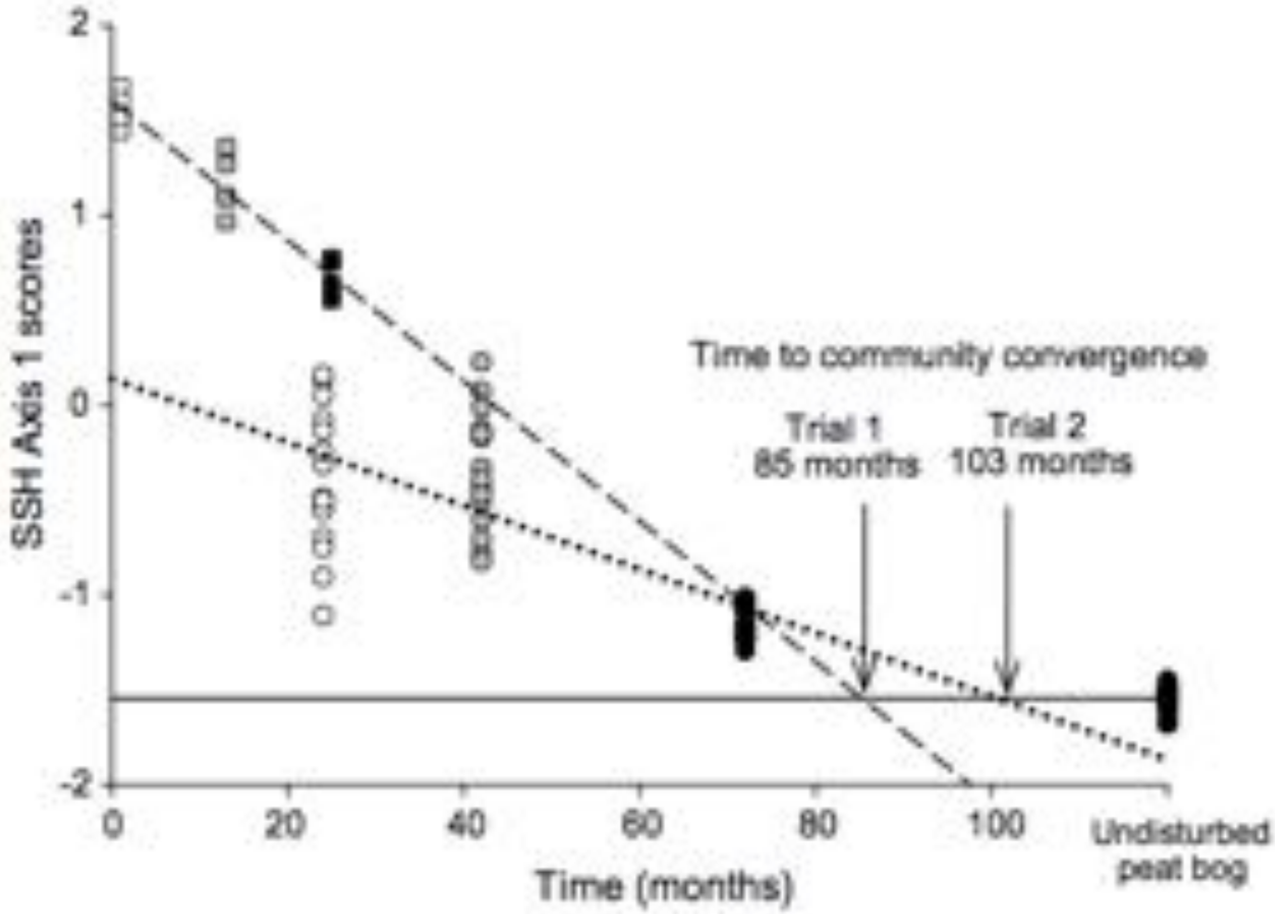
Translocate intact habitat

Assess effectiveness

Monitor beetle community – 88 spp

Watt 2008 Biol Conservation 141: 568-579

Axis describing beetle community



Conclusions from Restoration Ecology

Degraded ecosystems/communities can be rehabilitated

Restoration can restore ecosystem function

Complete restoration of communities is more difficult

Despite the damage humans have inflicted, ecosystems can recover from major perturbations

Restoration ecology is a discipline that can harness insights from community ecology