Communities

San Pedro Martir
(Baja, Mexico)

Corcovado National Park
(Costa Rica)

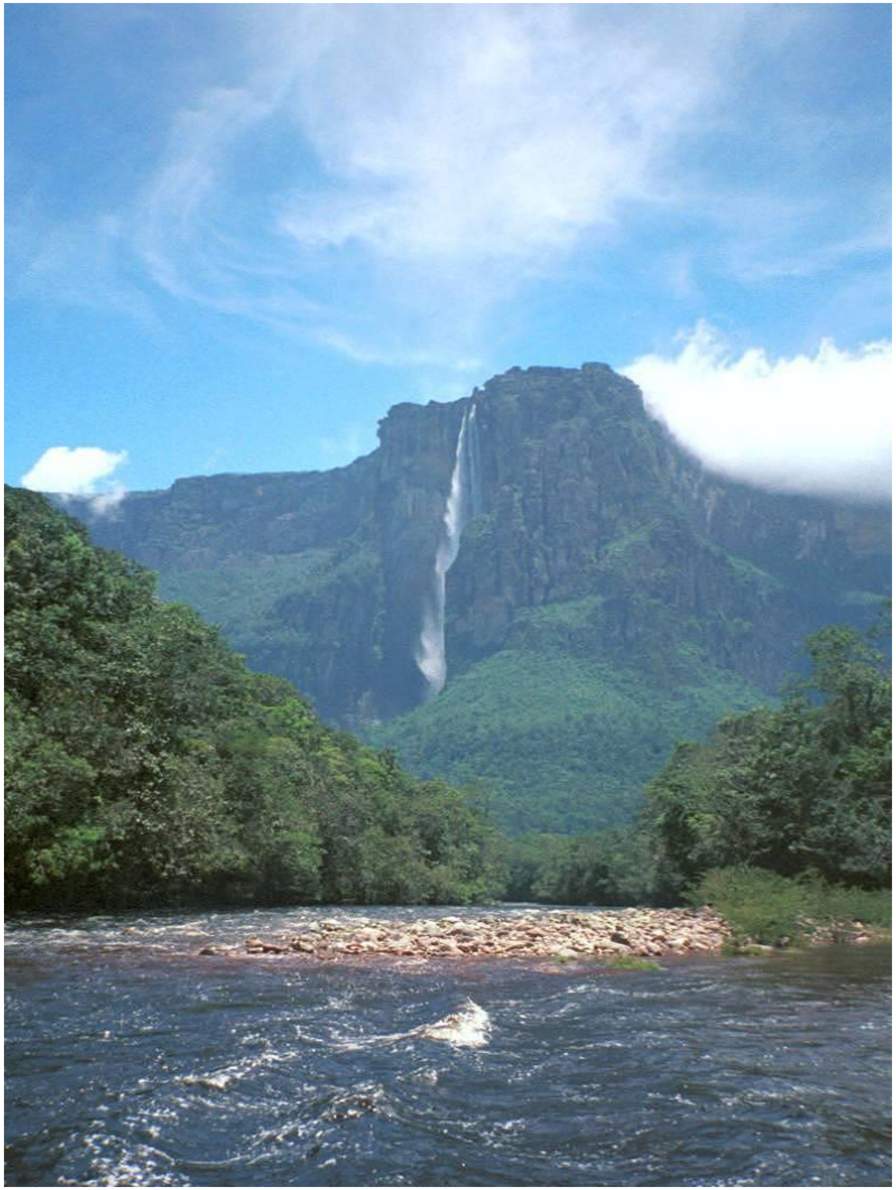
Colorado farm dirt

Chilcotin Mts
(British Columbia)

Communities

Creosote flats — Mojave desert
(*Larrea divaricata*)

Communities



Venezuelan rainforest (Angel Falls)

How can we quantify these differences?

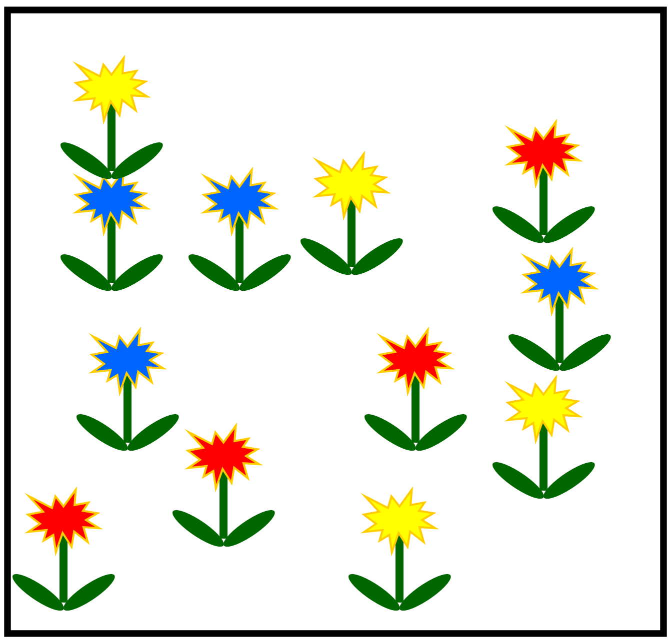
- **Species richness – The number of species per unit area**

- **Species evenness – The relative abundance of individuals among the species within an area**

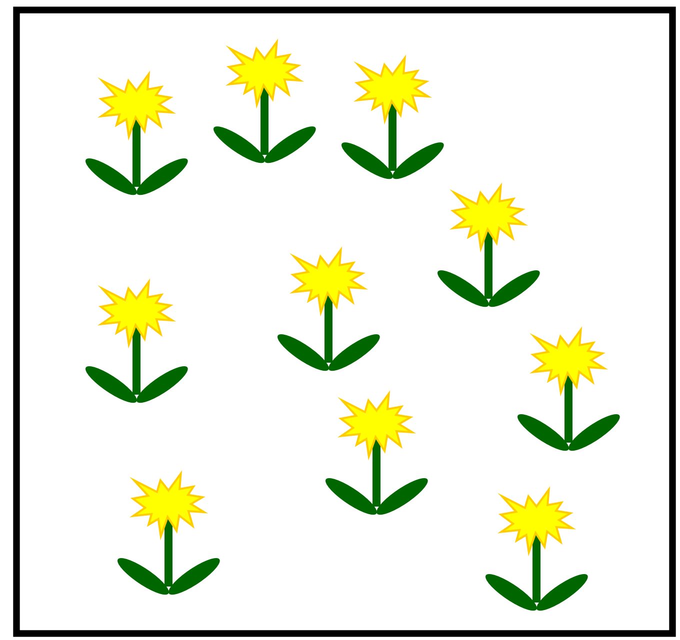
- **Species diversity – The combined richness and evenness of species within an area**

Species richness

- Simply count the number of species within a fixed area



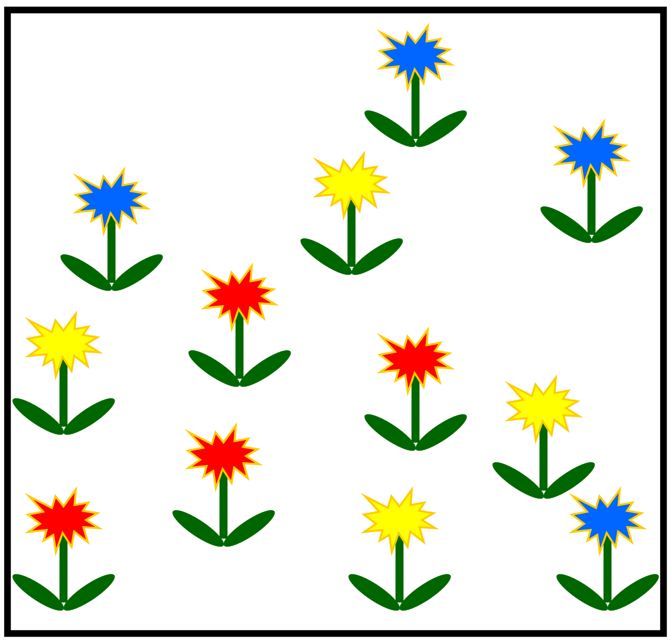
Richness = 3



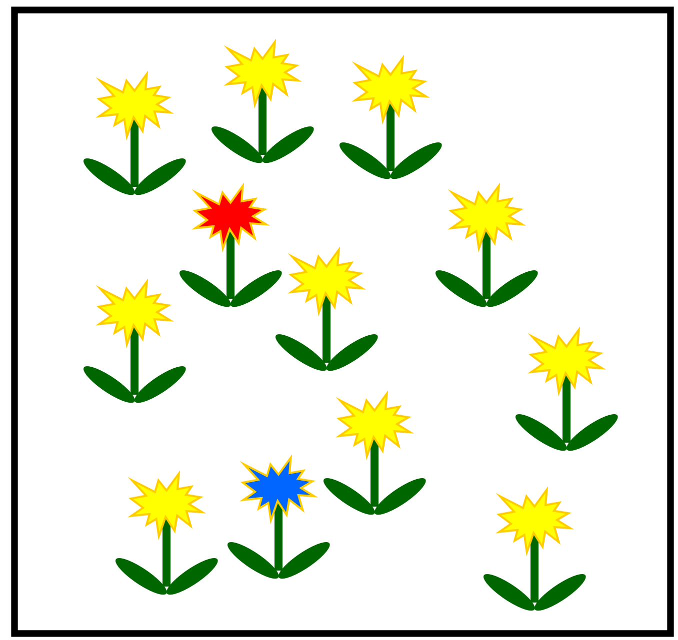
Richness = 1

A problem with species richness

- Species richness ignores species evenness



Richness = 3



Richness = 3

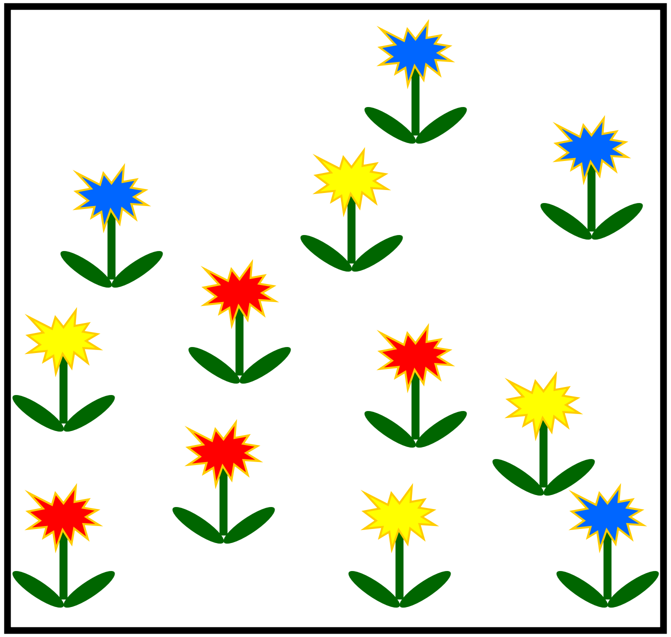
How can species evenness be incorporated?

Species diversity – Measures both species richness and evenness

The Shannon Index:

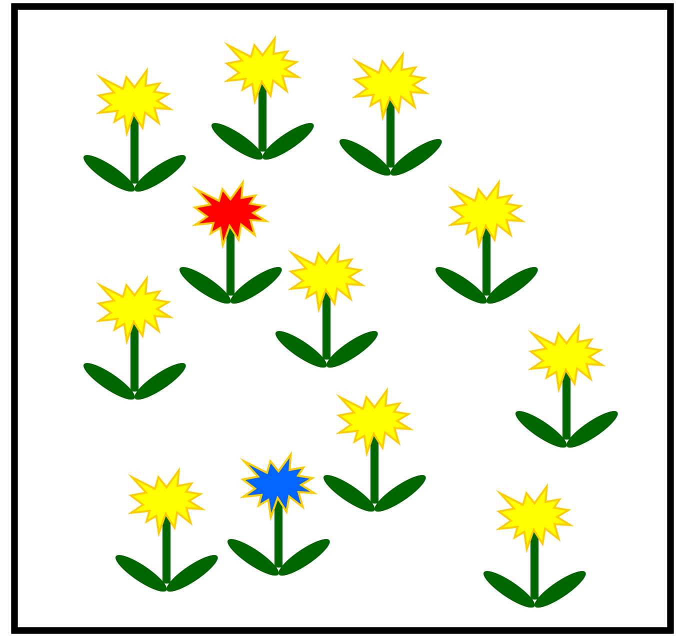
$$H = -\sum_{i=1}^{n} (p_i)(\ln p_i)$$

How do you use the Shannon Index?



Species Name	N_i	p_i	$\ln(p_i)$
Species 1 (red)	4	.333	-1.10
Species 2 (blue)	4	.333	-1.10
Species 3 (yellow)	4	.333	-1.10
Total:	12	1	--

H =-[.333(-1.10) +. 333(-1.10) +. 333(-1.10)] =1.10

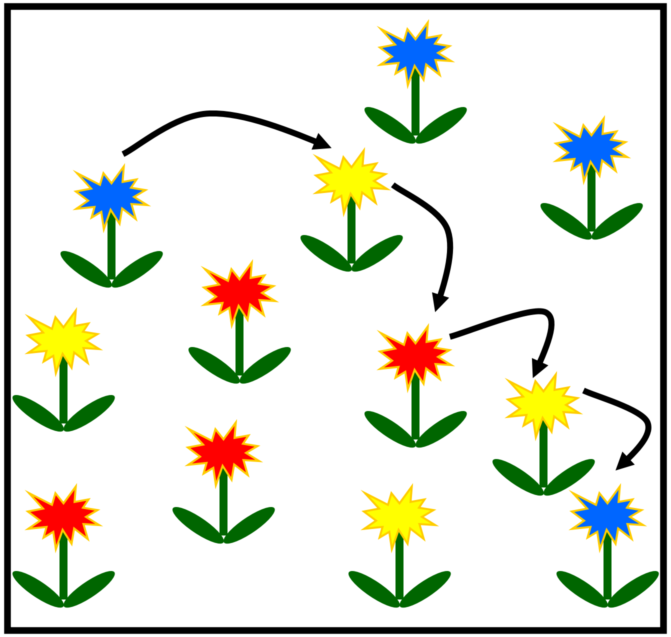


Species Name	N_i	p_i	$\ln(p_i)$
Species 1 (red)	1	.083	-2.49
Species 2 (blue)	1	.083	-2.49
Species 3 (yellow)	10	.833	-0.18
Total:	12	1	--

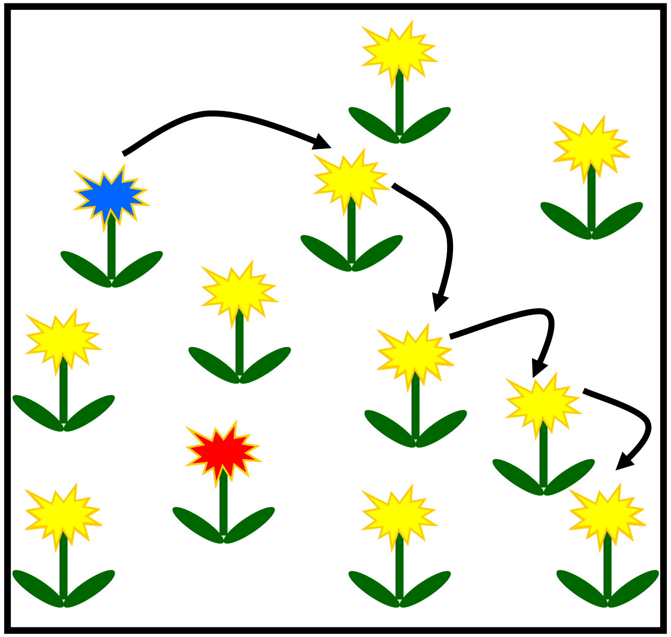
H =-[.083(-2.49) +. 083(-2.49) +. 833(-.18)] = 0.56

What does the Shannon Index really tell us?

• The greater the value of H the greater the likelihood that the next individual chosen will not belong to the same species as the previous one



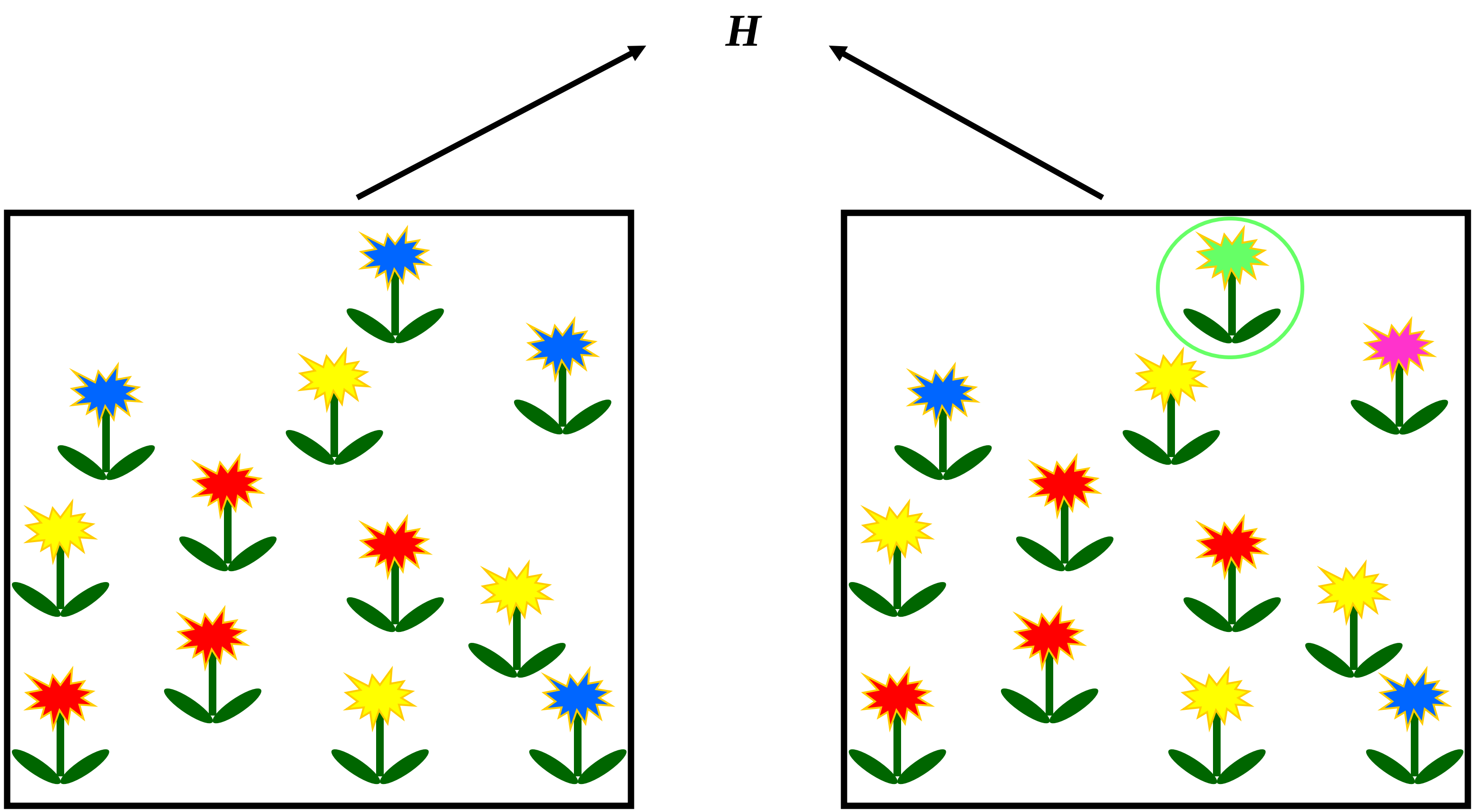
$H = 1.10$



$H = 0.56$

A problem with diversity indices

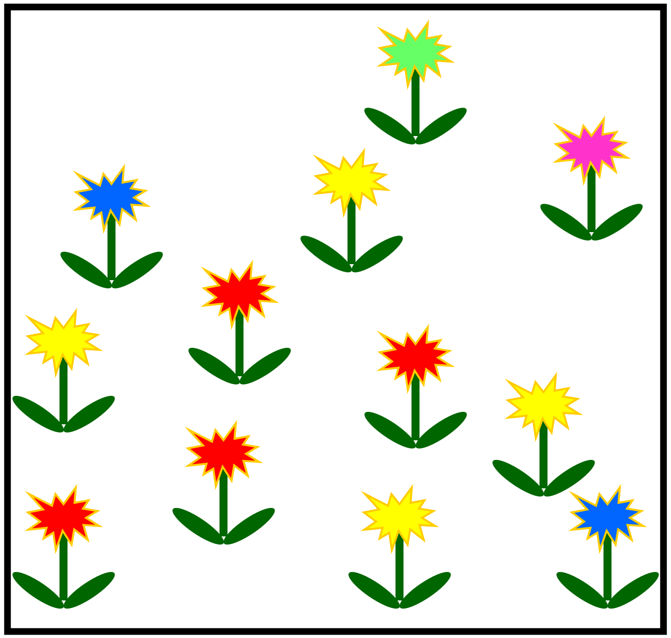
• Two communities with the same diversity index do not necessarily have the same species richness and evenness



Bottom Line: Information is lost when a community is described by a single number!

A graphical solution: rank-abundance curves

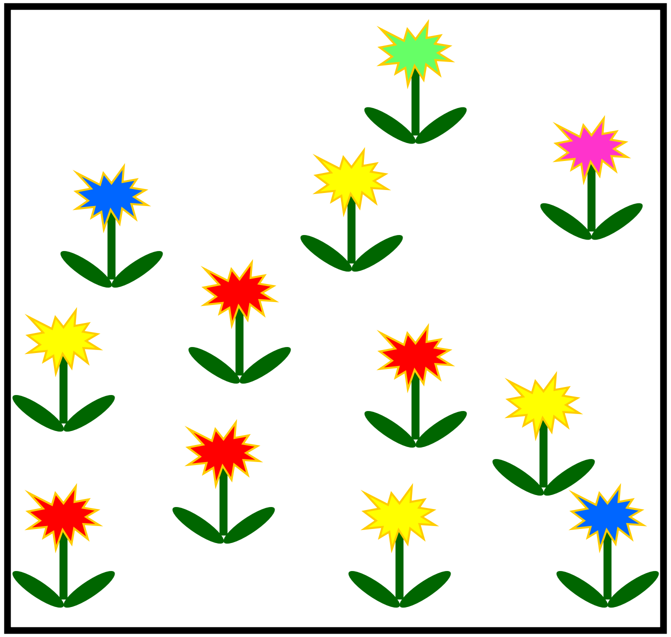
Step 1: Count the numbers of each species within a defined area



Species Name	$\mathbf{N_i}$
Species 1 (red)	4
Species 2 (yellow)	4
Species 3 (blue)	2
Species 4 (pink)	1
Species 5 (green)	1
Total:	12

Rank-abundance curves

Step 2: Calculate the frequency of each species

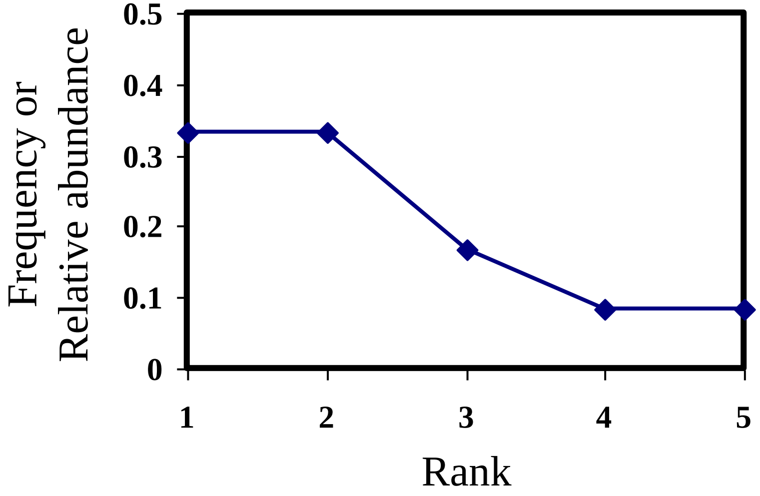


Species Name	**N_i**	**p_i**
Species 1 (red)	4	.333
Species 2 (yellow)	4	.333
Species 3 (blue)	2	.167
Species 4 (pink)	1	.083
Species 5 (green)	1	.083
Total:	12	1

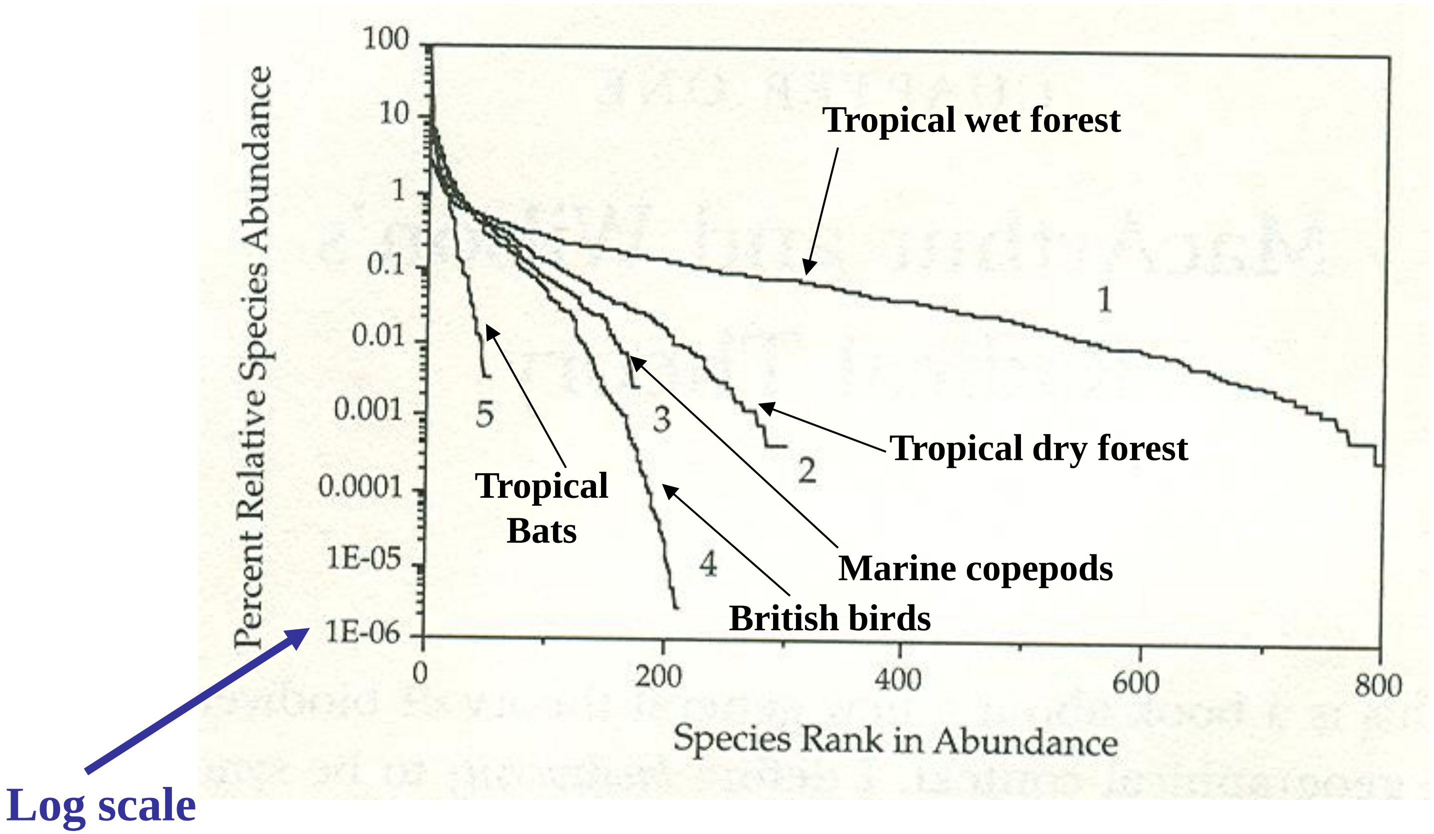
Rank-abundance curves

Step 3: Plot the species frequencies as a function of frequency rank

Species Name	$\mathbf{N_i}$	$\mathbf{p_i}$
Species 1 (red)	4	.333
Species 2 (yellow)	4	.333
Species 3 (blue)	2	.167
Species 4 (pink)	1	.083
Species 5 (green)	1	.083
Total:	12	1



A general pattern in rank-abundance

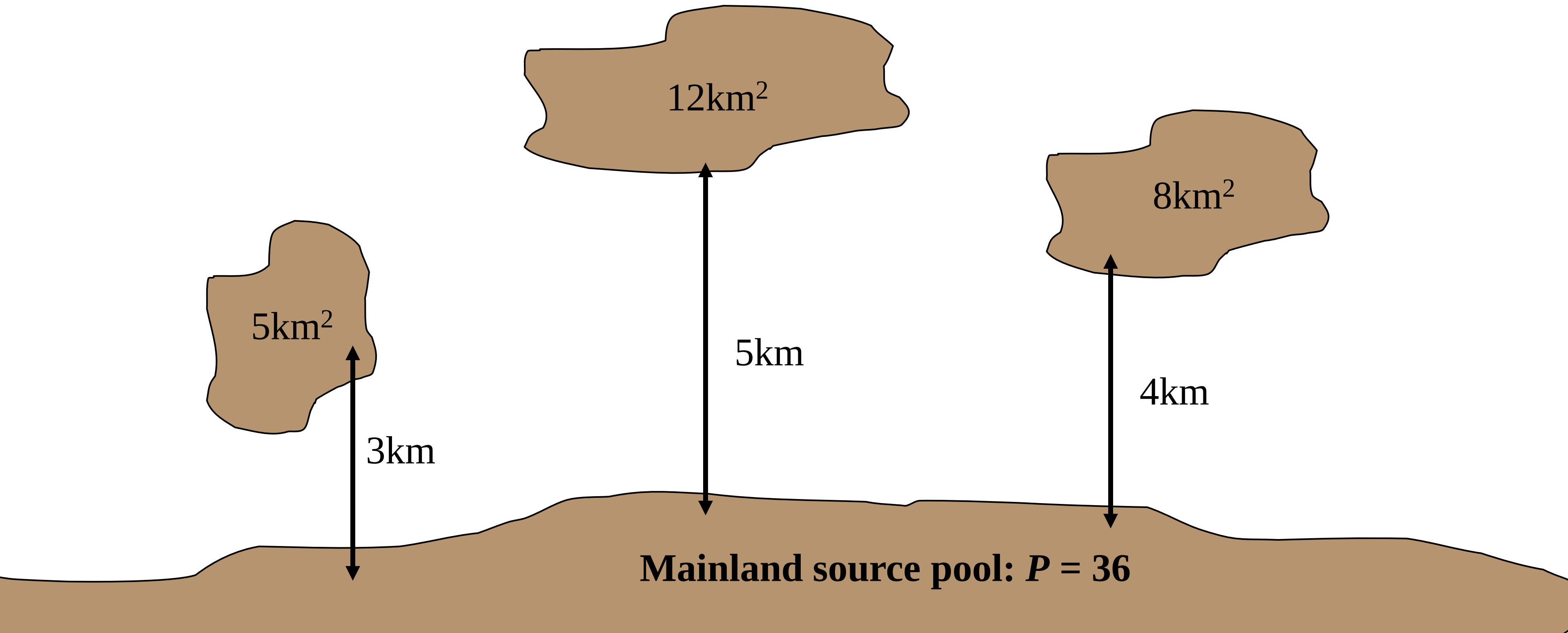


A consistent result: Coexistence of multiple ecologically similar species

Applying the theory to reserve design

(A practice problem)

- You are tasked with selecting between three potential locations for a new national park
- Your goal is to maximize the long term species richness of passerine birds within the park
- Previous research has shown that the birds meet the assumptions of the equilibrium model

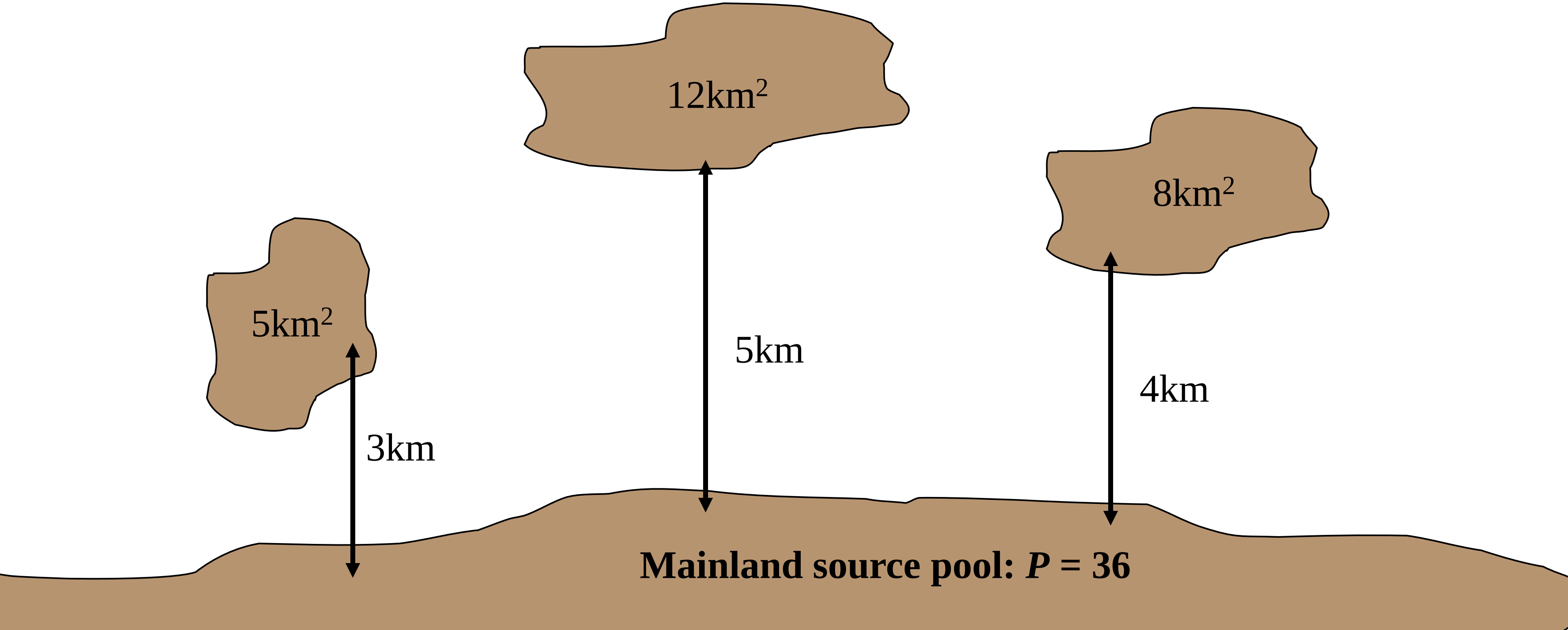


Applying the theory to reserve design

(A practice problem)

<u>Previous research has also shown that:</u>

- $I = 2/x$ where x is distance to the mainland
- $E = .4/A$ where A is the area of the island
- Which of the three potential parks would best preserve passerine bird species richness?



What explains persistence of multiple species?

- Multiple ecologically similar species often coexist within communities

- Superficially, this is inconsistent with the “competitive exclusion principle”

  → We know that resources are, at least in some cases limiting
  → We know that limited resources lead to competition
  → Lotka-Volterra tells us that ecologically similar species are unlikely to coexist

- What forces maintain species diversity within communities?

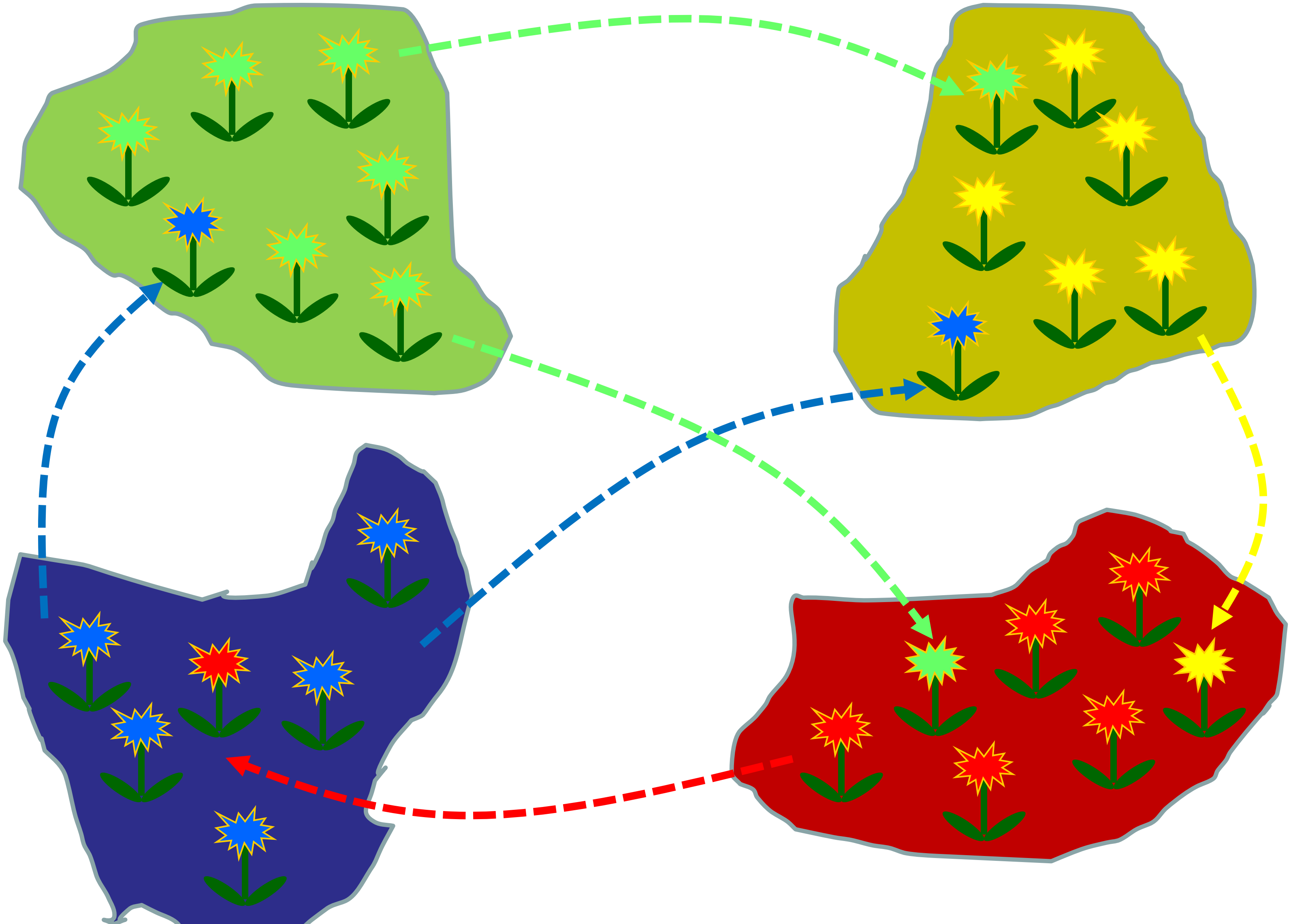
What explains persistence of multiple species?

- **Spatio-Temporal variability and the Intermediate Disturbance Theory**

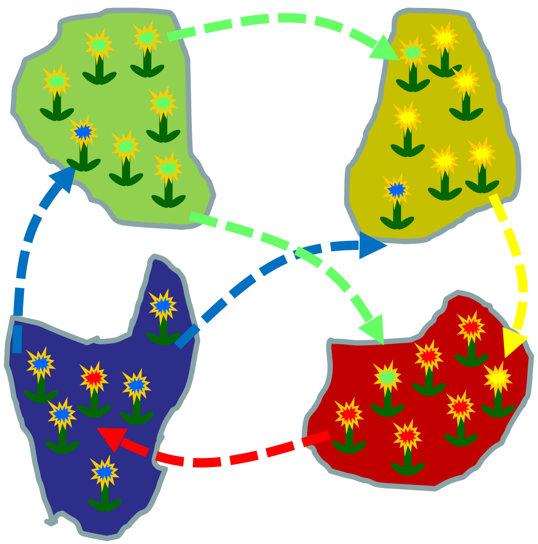
- **Interactions with grazers and predators**

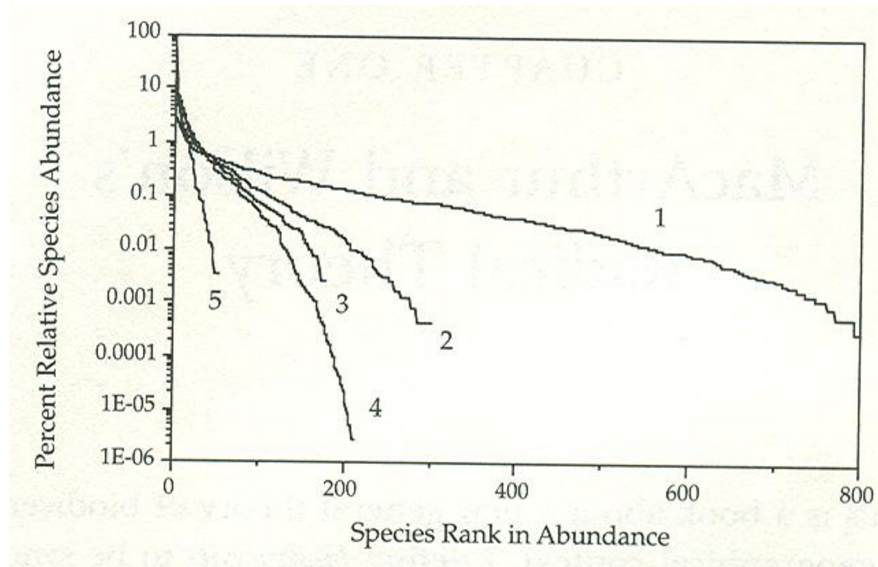
- **Neutral theory**

Spatial variability



Spatial variability and dispersal are insufficient

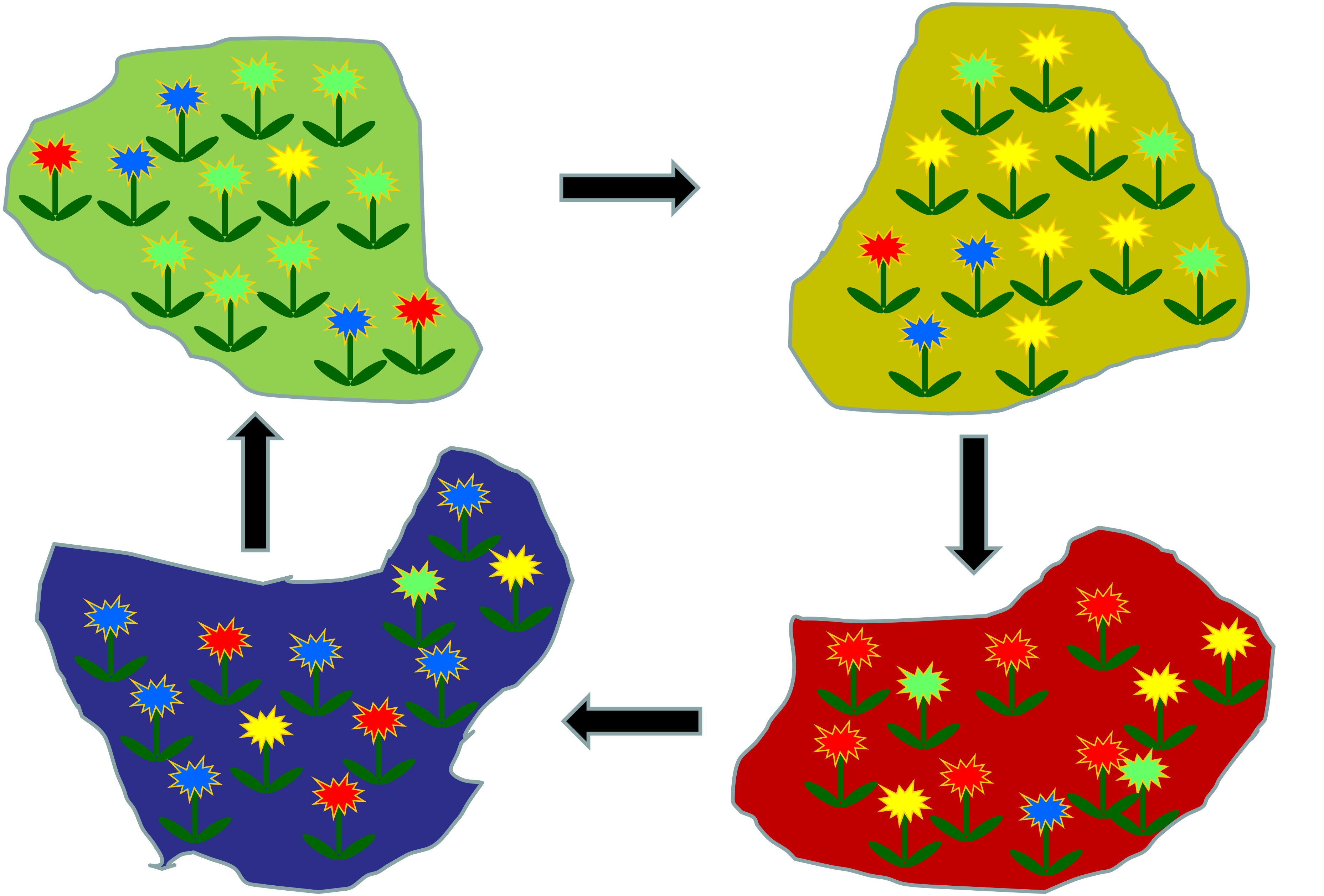




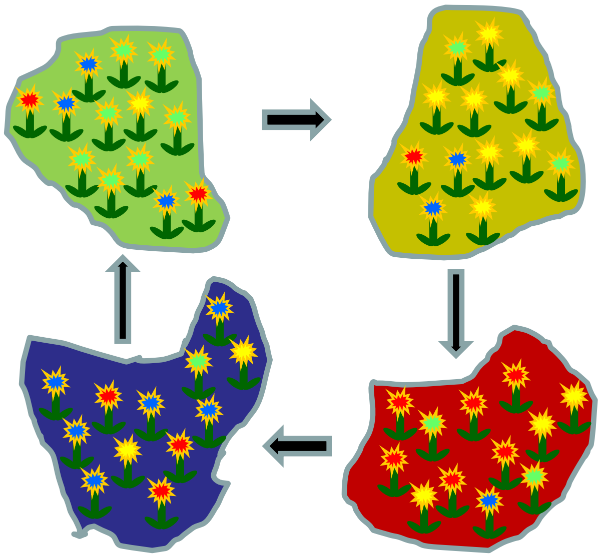
- Unless dispersal is very high or competition very weak, communities will consist of a single dominant species and many very rare species

- This is not what we see in real data

Temporal variability



What causes temporal variability?



- **Disturbance opens up new, unoccupied, habitats**

The process of succession: Glacier Bay N.P.

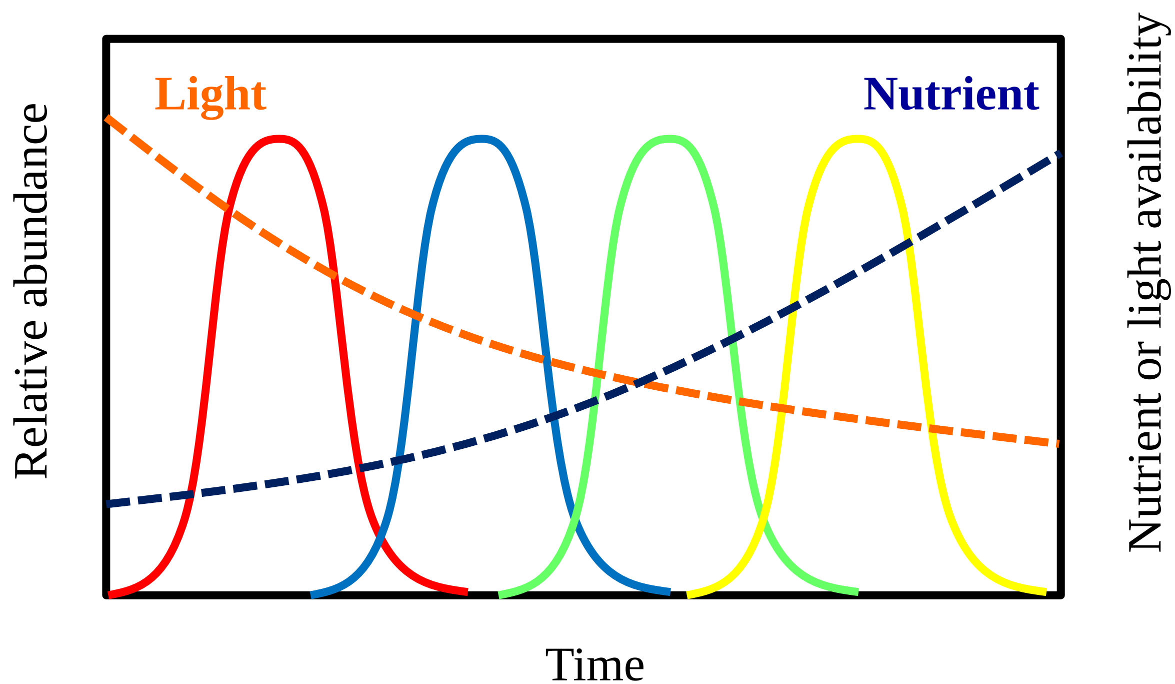
- **Glaciers have been continually receding**
- **Unoccupied habitat is continually appearing**
- **Process has been studied for the past 80 years**

Step 1	**Step 2**	**Step 3**	**Step 4**
• Colonization by mosses, *Dryas*, and willow • *Dryas* fixes nitrogen increasing nitrogen content of soil	• Colonization by *Alnus*; *Dryas* and willow displaced • *Alnus* species fix nitrogen and acidify the soil	• Colonization by Sitka spruce; *Alnus* displaced • Spruce increases carbon content of soil improving aeration and water retention	• Colonization by Hemlock • No further change; Spruce-Hemlock forest persists indefinitely

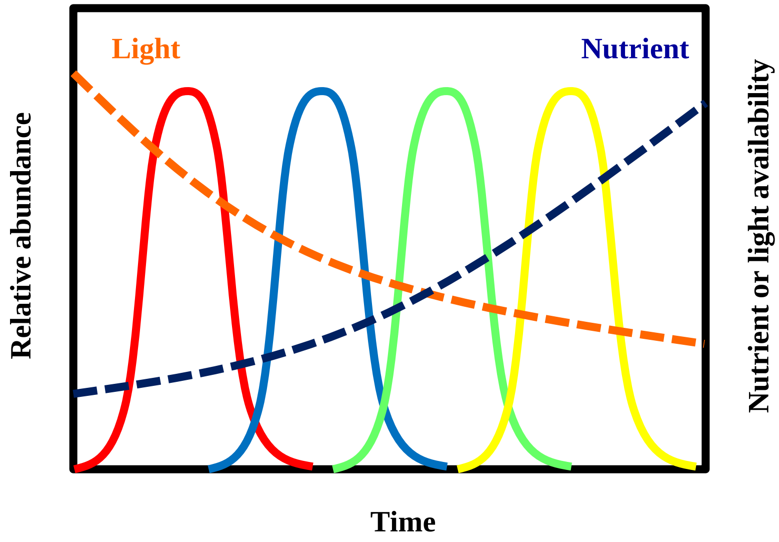
A model of succession

- **The resource ratio hypothesis (Tillman, 1988)**

Species 1	Species 2	Species 2	Species 2
• Requires minimal nutrient	• Requires moderate nutrient	• Requires significant nutrient	• Requires abundant nutrient
• Requires high light	• Requires medium-high light	• Requires medium light	• Requires minimal light



Temporal variability alone is insufficient



- Only several of all possible species generally coexist at any point in time
- Species coexistence is transient → ultimately one dominant species prevails

The intermediate disturbance hypothesis
(Connell, 1978)

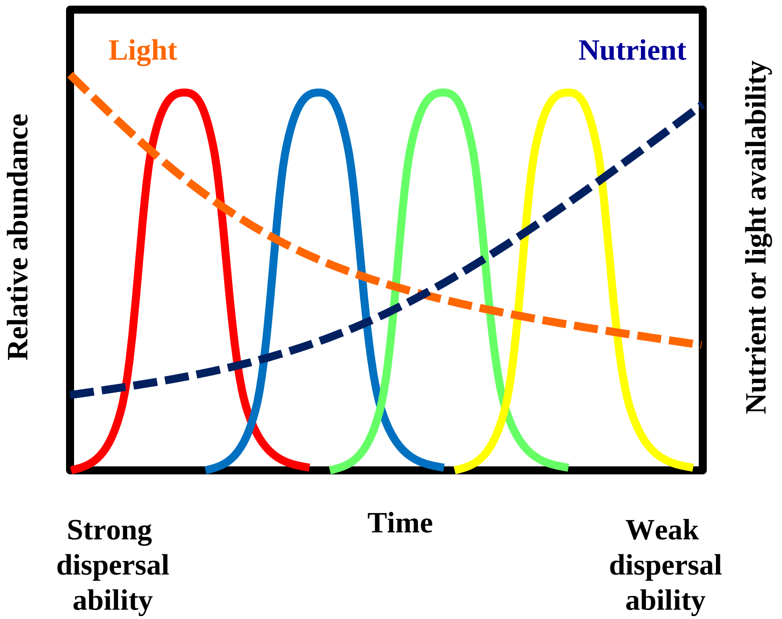
<u>Assumptions of the IDH</u>

• Species differ in their dispersal ability

• Pioneer species require few nutrients, high light, and disperse well (r selected)

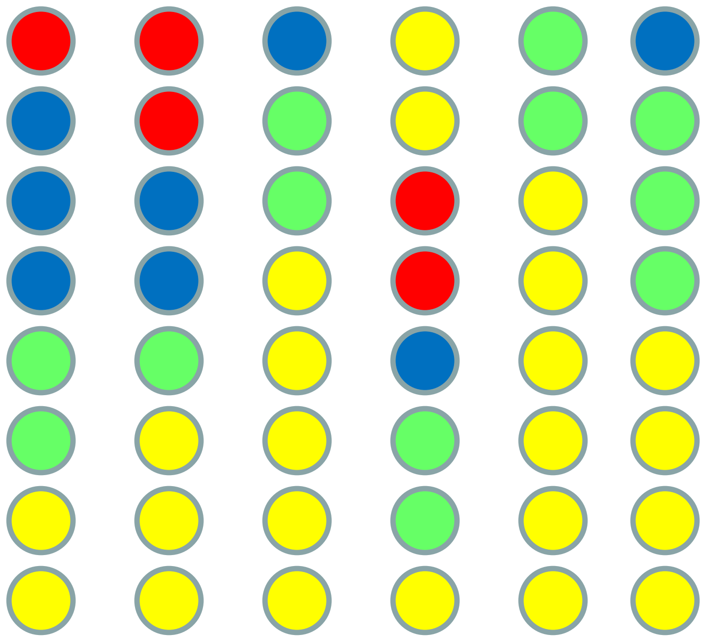
• Late successional species require abundant nutrients, low light, and disperse poorly (k selected)

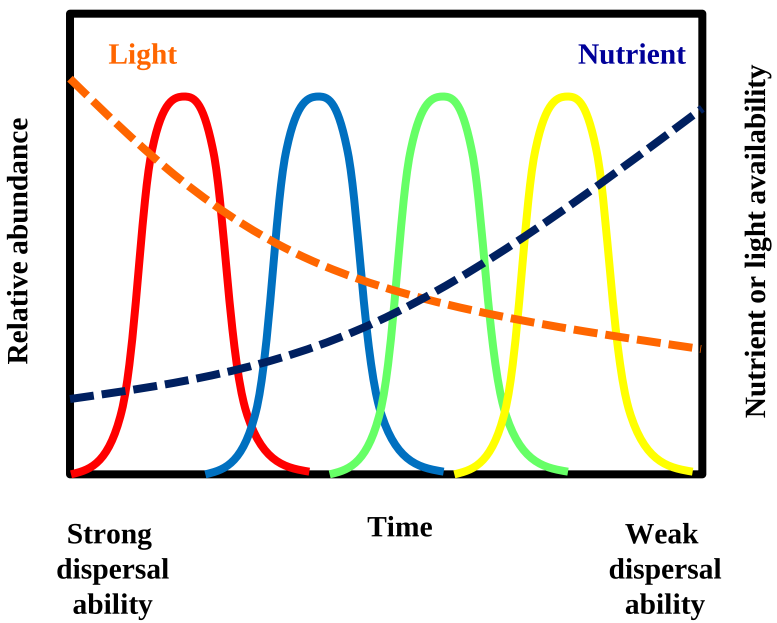
• Repeated disturbances occur (e.g., Fire, logging, landslides, flooding, etc.)



The intermediate disturbance hypothesis
(Connell, 1978)

<u>If the disturbance rate is too low</u>

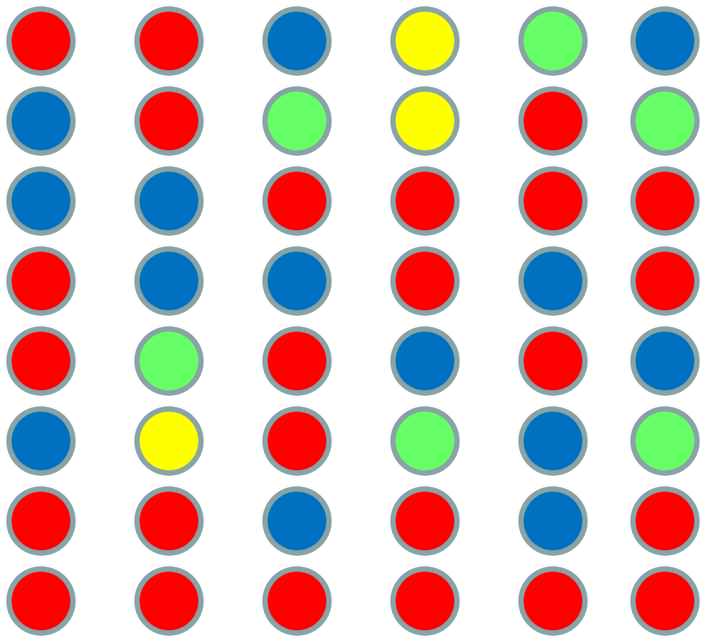


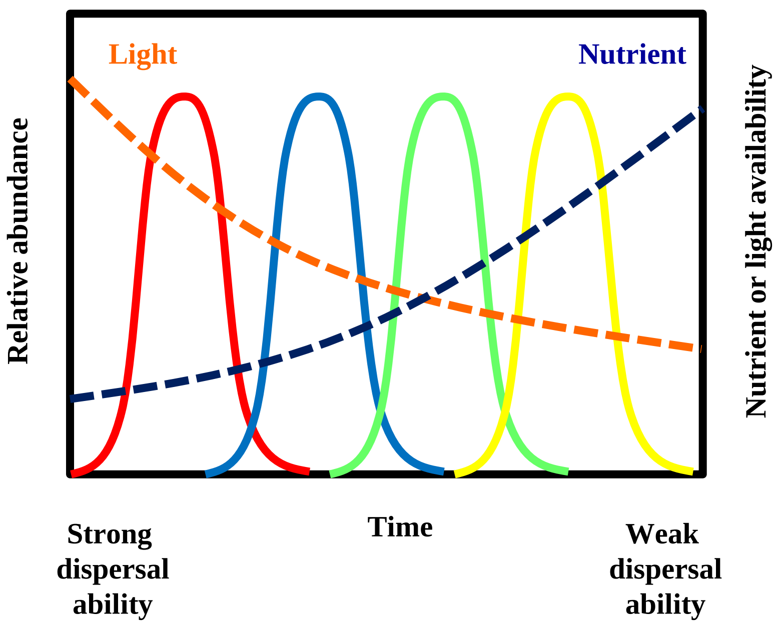


• Only a single late successional species remains. All other species extinct.

The intermediate disturbance hypothesis
(Connell, 1978)

<u>If the disturbance rate is too high</u>

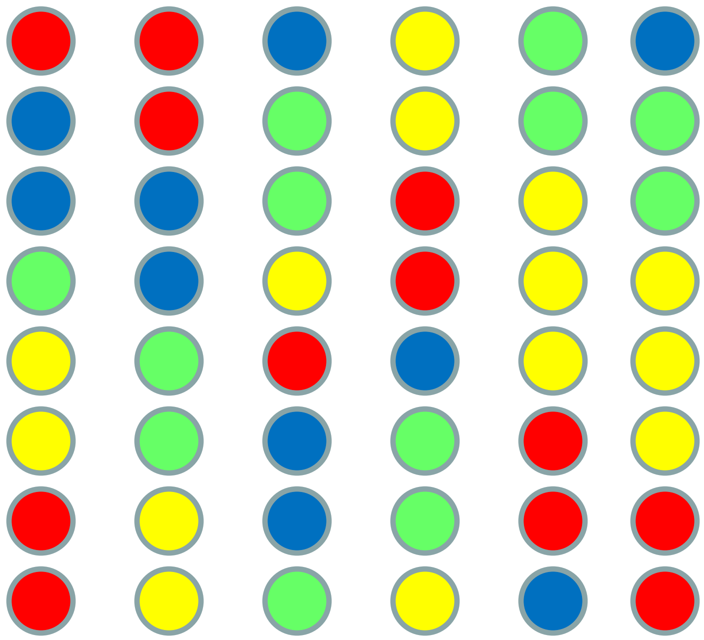


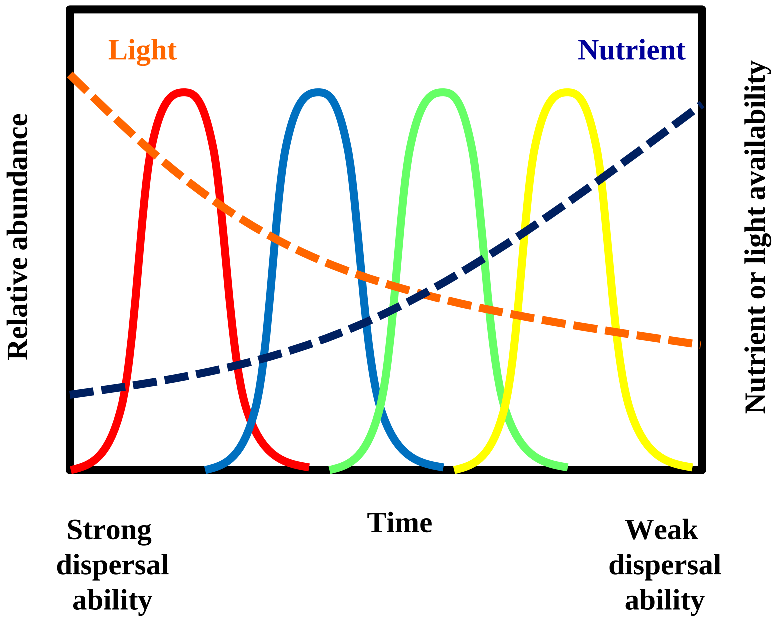


• Only a pioneer species remains. All other species extinct.

The intermediate disturbance hypothesis
(Connell, 1978)

<u>If the disturbance rate is intermediate</u>





• All species remain

A test of the IDH: Intertidal algal communities
(Sousa, 1979)

<u>First studied succession in the absence of disturbance</u>

• Studied algal succession on intertidal boulders

• Scraped natural rocks clean

• Implanted concrete blocks

• Found a stereotypical pattern

<u>Steps in algal succession</u>

1. Initially colonized by the green alga *Ulva*
2. Later colonized by four species of red alga
3. Within 2-3 years each rock or block is a monoculture covered by a single species of red algae

A test of the IDH: Intertidal algal communities
(Sousa, 1979)

Next, studied succession in the presence of disturbance

• Calculated the wave force needed to roll each boulder at study site

• Classified boulders according to force required to move them, an index of "disturbability"

• Calculated algal species richness on all boulders

Results

1. Amount of bare (uncolonized space) decreased with boulder size
   → confirms that larger boulders were disturbed less

2. Species richness was greatest on boulders in the intermediate size class
   → Supports the IDH

Interactions with grazers and predators

- **Grazing and predation reduce biomass of graze or abundance prey**

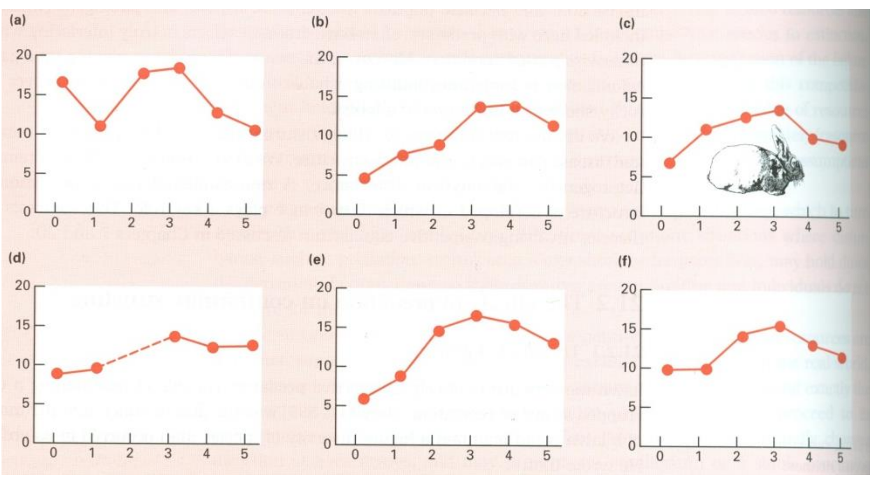
- **Can be viewed as a form of disturbance**

Grazing and species diversity

Zeevalking and Fresco (1977)

- Studied impact of rabbit grazing on flora of sand dunes in the Netherlands
- Estimated the intensity of rabbit grazing in $1 m^2$ plots located on five different sand dunes
- Estimated the species richness in each plot

Species richness



Grazing pressure

- Grazing increased species richness
- Species richness was maximized at intermediate grazing intensities

Predation and species diversity

Pisaster ochraceus
(Ochre star fish)

Rocky intertidal — Washington coast

Pisaster are major predators of the intertidal

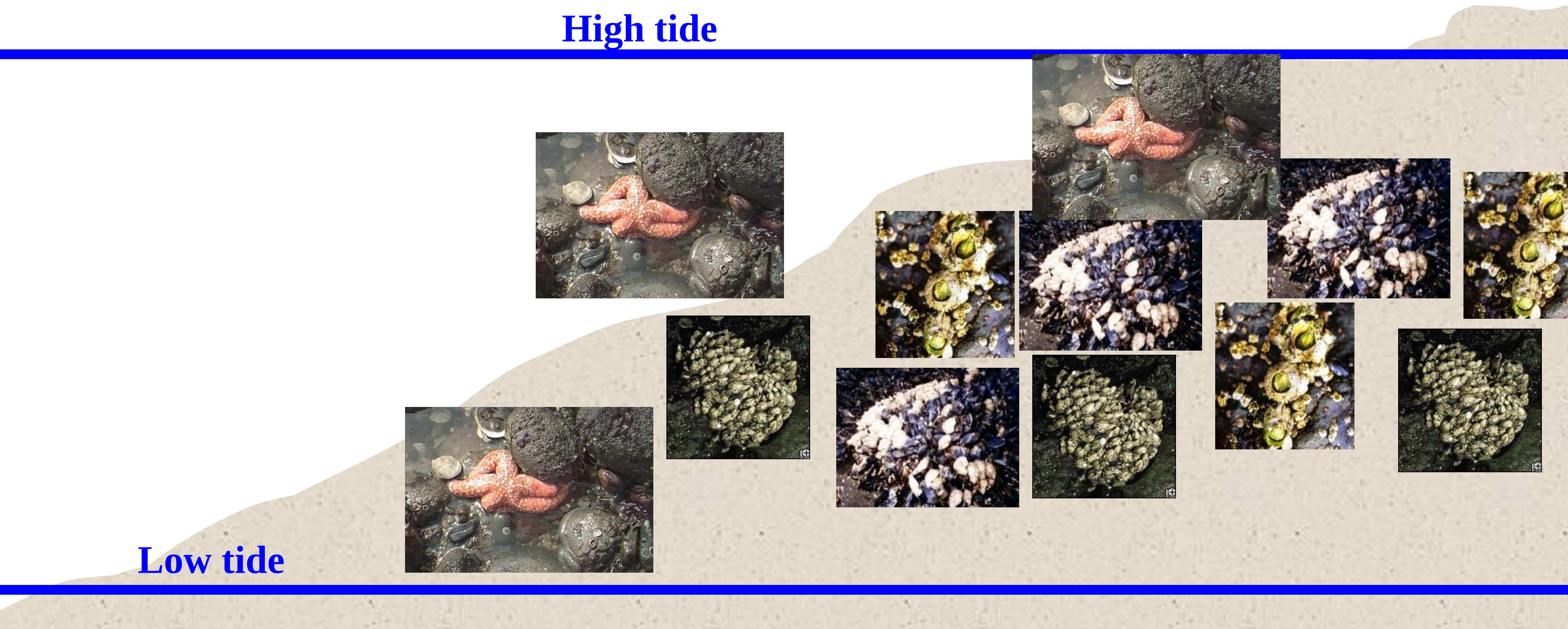
Mytilus californianus
(California blue mussel)

Balanus glandula
(Acorn Barnacle)

Mitella polymerus
(Gooseneck barnacle)

Pisaster ochraceus
(Ochre star fish)

Under natural conditions, all 3 prey species occur



A classic experiment
(Paine, 1966)

- Established two study plots in the rocky-intertidal zone of Mukkaw Bay, Washington on June 1963

- In one plot *Pisaster* was removed

- The other plot acted as an unmanipulated control

Species richness actually declined

- By September of 1963 *Balanus glandula* occupied 80% of the available space

- By June of 1964 *Balanus* had been almost completely displaced by *Mytilus californianus*

- In contrast to the plot where *Pisaster* had been removed, the control plot maintained a steady level of species richness with all three prey species present

- These results demonstrate that the predatory starfish, *Pisaster*, actually maintained prey species richness!

Why did this occur?

• *Pisaster* is a major predator of the three competing intertidal organisms

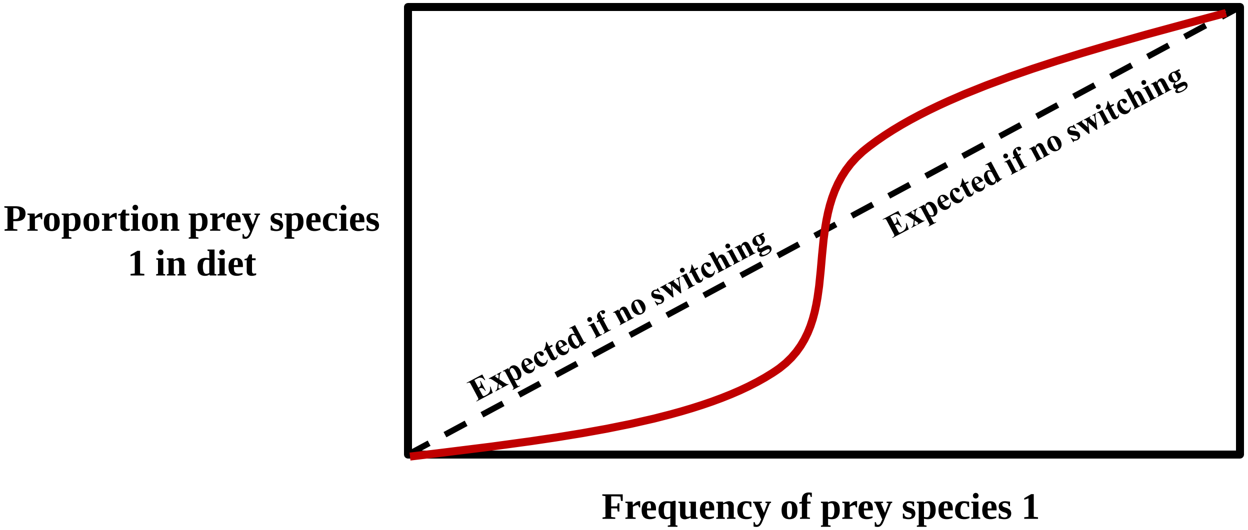
• In the absence of predation by *Pisaster* the superior competitor excludes all other species (competitive exclusion)

• In the presence of *Pisaster*, however, the density of the best competitor is limited by predation, allowing coexistence

• *Pisaster* acts as a **keystone predator,** playing a significant role in shaping community structure

Diet switching and frequency dependence

• Predators and grazers may actively switch from rare to common prey



• Generates *negative frequency dependence*

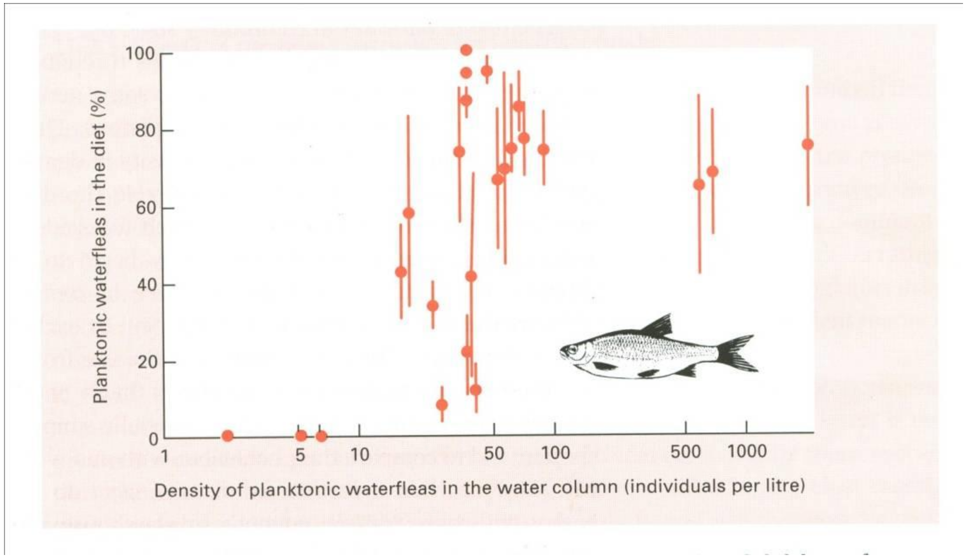
• Promotes coexistence of multiple prey species

Diet switching: Zooplanktivorous fish

Townsend et al. (1986)

- Studied feeding behavior of the roach, *Rutilus rutilus*, in a small English lake
- Fish prefer planktonic waterfleas when available
- Switch to sediment dwelling waterfleas when planktonic waterfleas are rare

Rutilus rutilus



Neutral theory of biodiversity

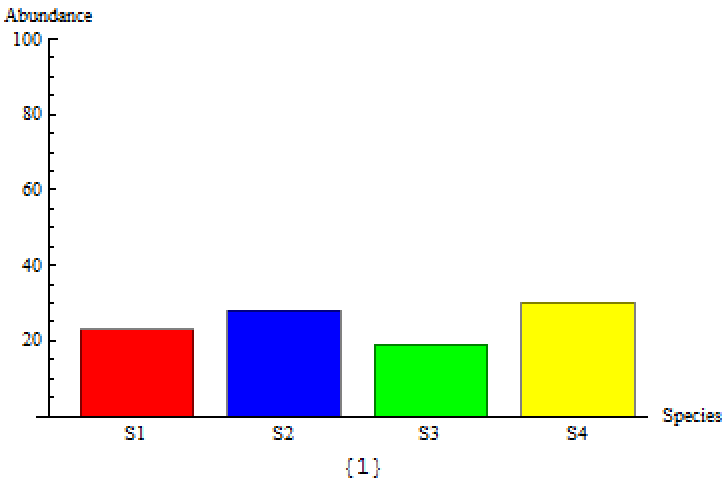
Hubbell (2001)

• Assume that all species are competitively equivalent

• In other words, all species within a guild are interchangeable

• Assume species have finite population sizes

• Under these conditions, the frequency of species within a habitat changes at random



Neutral theory of biodiversity

Hubbell (2001)

- Assume that new species are formed at a fixed rate

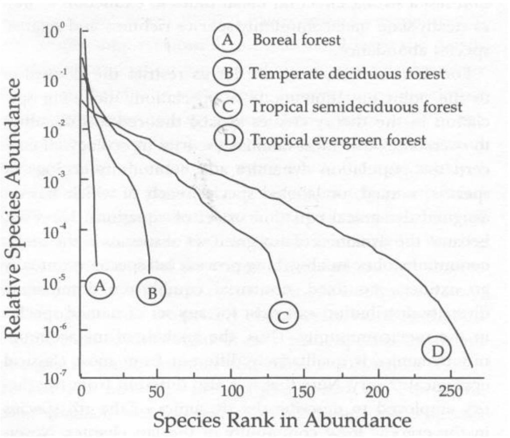
- Assume that dispersal occurs between habitats

- Essentially a model of random genetic drift with mutation and gene flow!!!

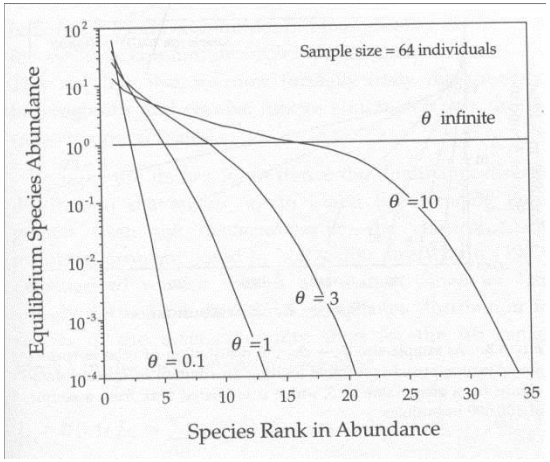
Neutral theory of biodiversity

Hubbell (2001)

• **Predictions of this simple model fit the data well**



• **In fact, they fit as well as more complicated models**



• **Yet, we know the assumptions of the model are wrong**

- ➢**Species are not competitively equivalent**
- ➢**Species do exhibit niche differentiation**