A vibrant underwater photograph showing a coral reef in the foreground with various colorful corals like yellow, green, and white. In the background, several small fish are swimming near a large, overhanging rock formation covered in green algae.

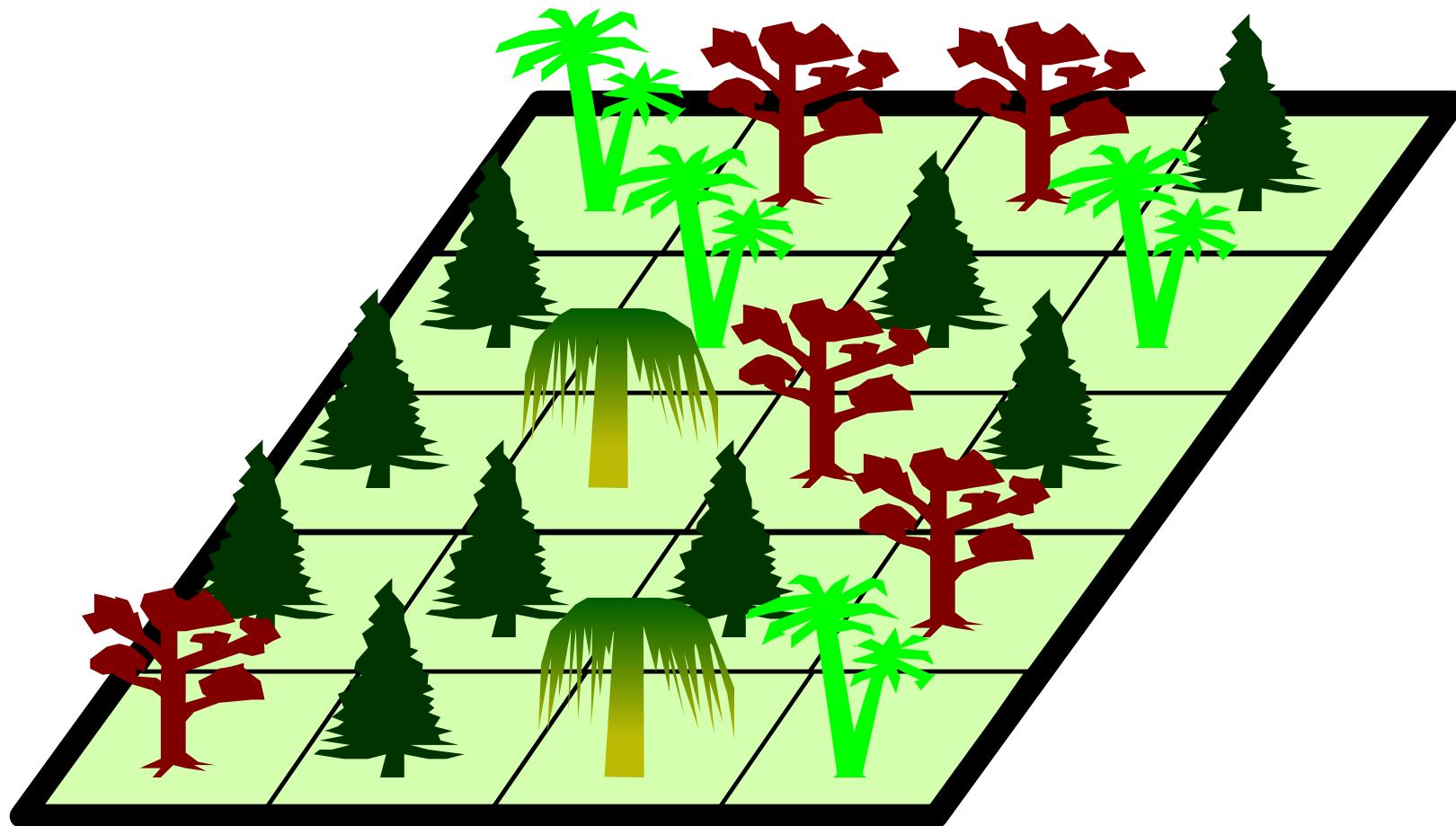
# Mop up and applications of neutral theory in ecology and evolution

James Rosindell

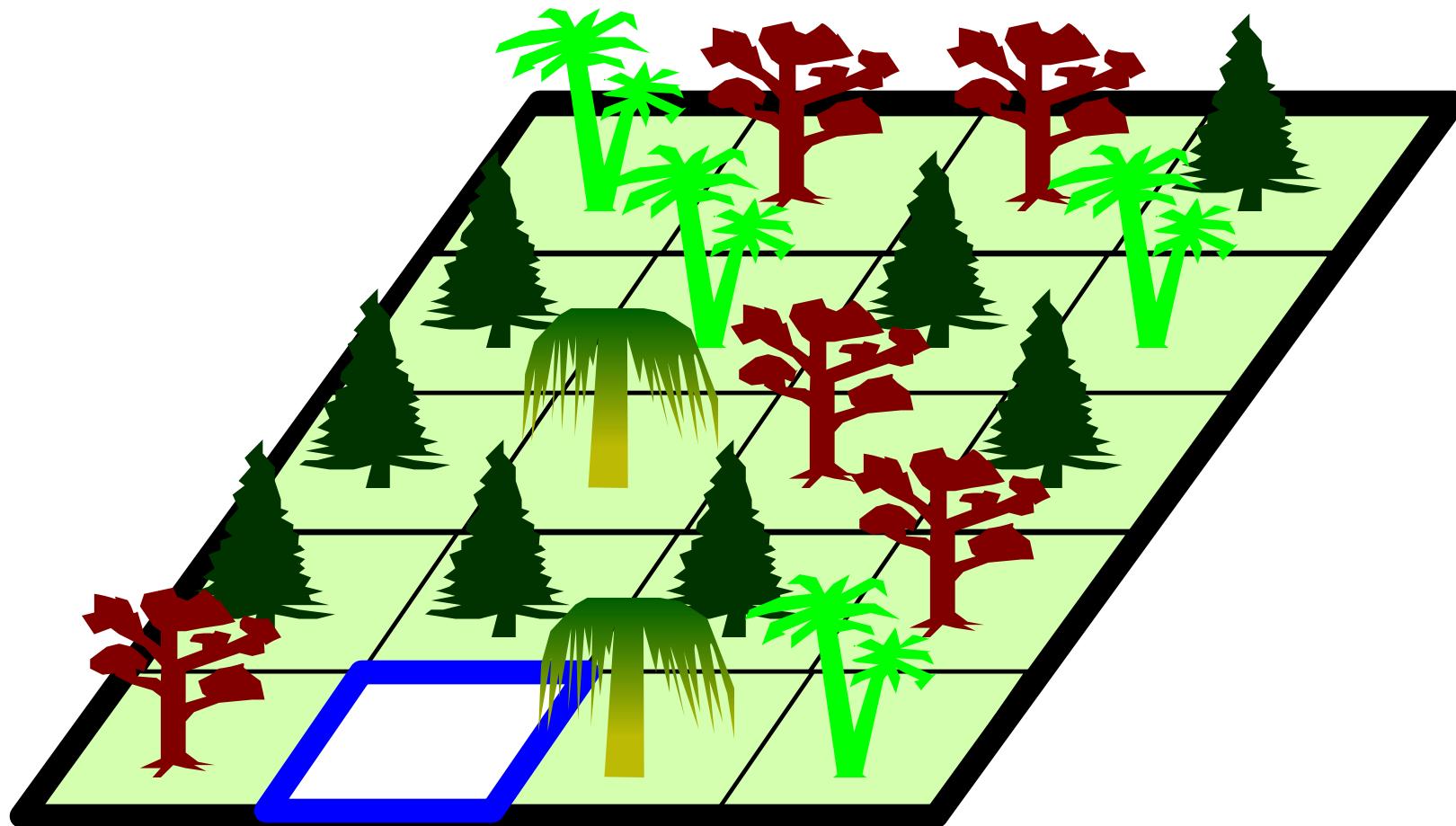
# Contents

- Coalescence methods in neutral theory
- Eigen Vectors and Eigen Values intuition
- Extinction debt and habitat fragmentation example

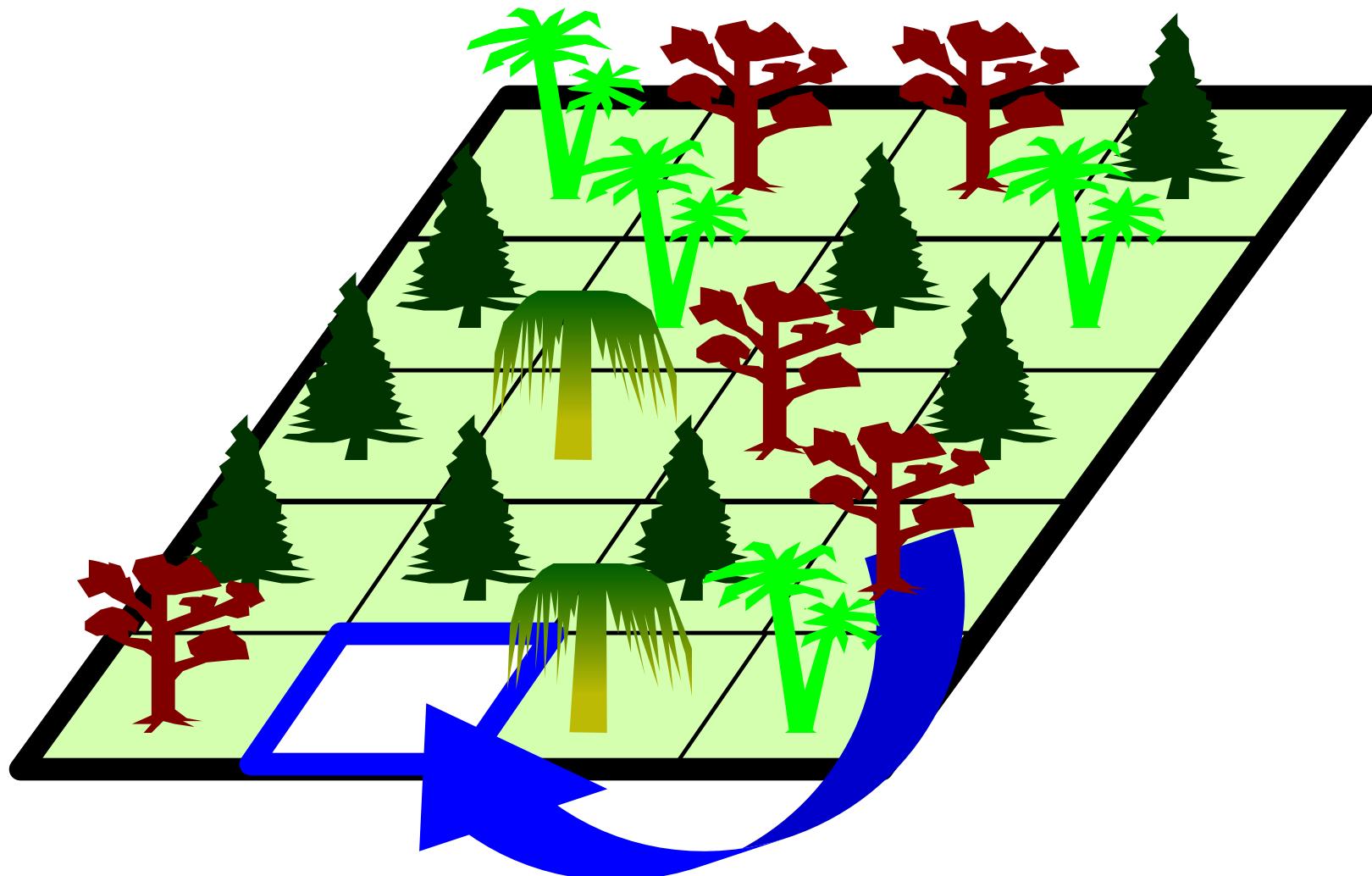
# The model rules in brief



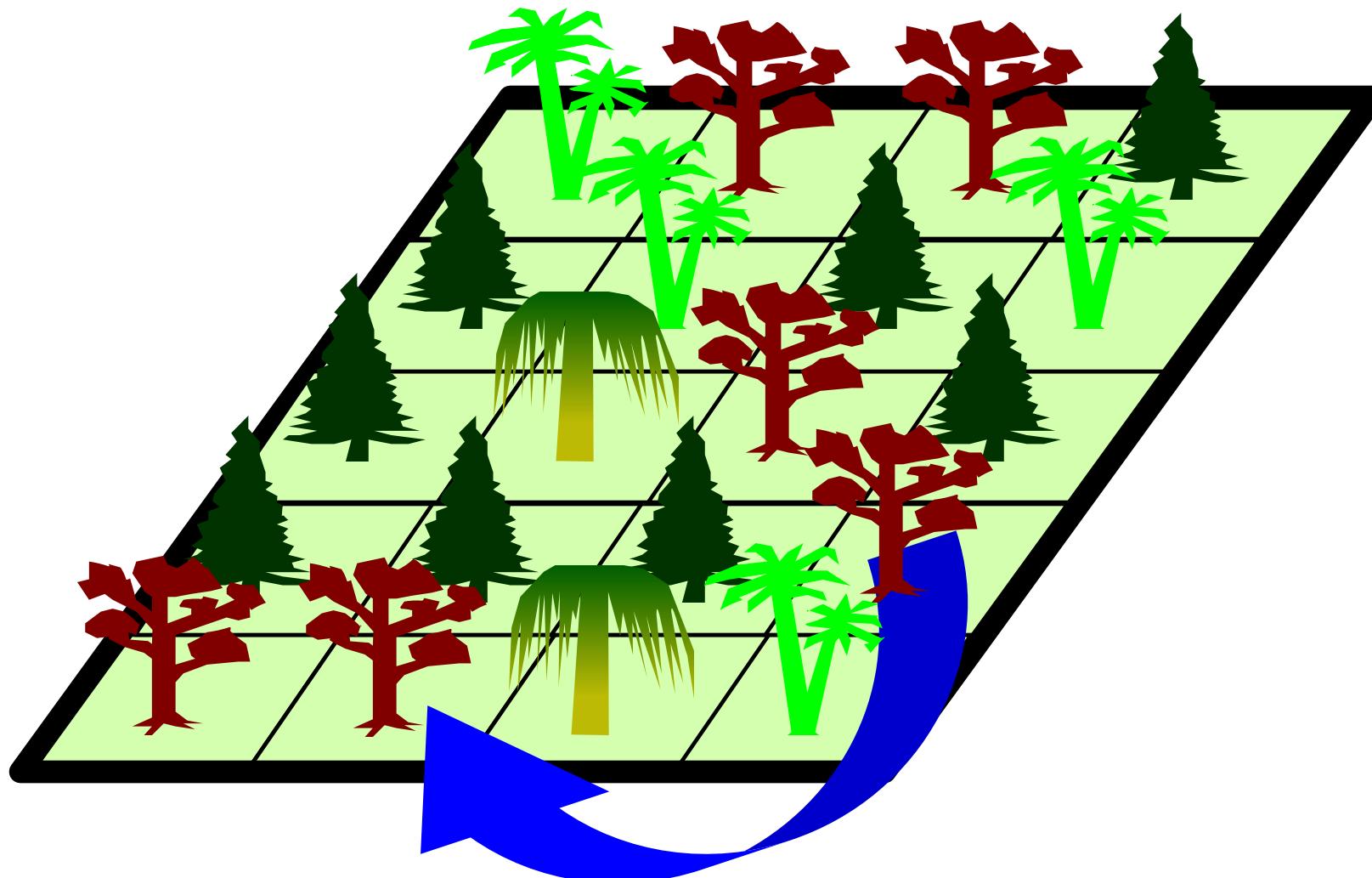
# The model rules in brief



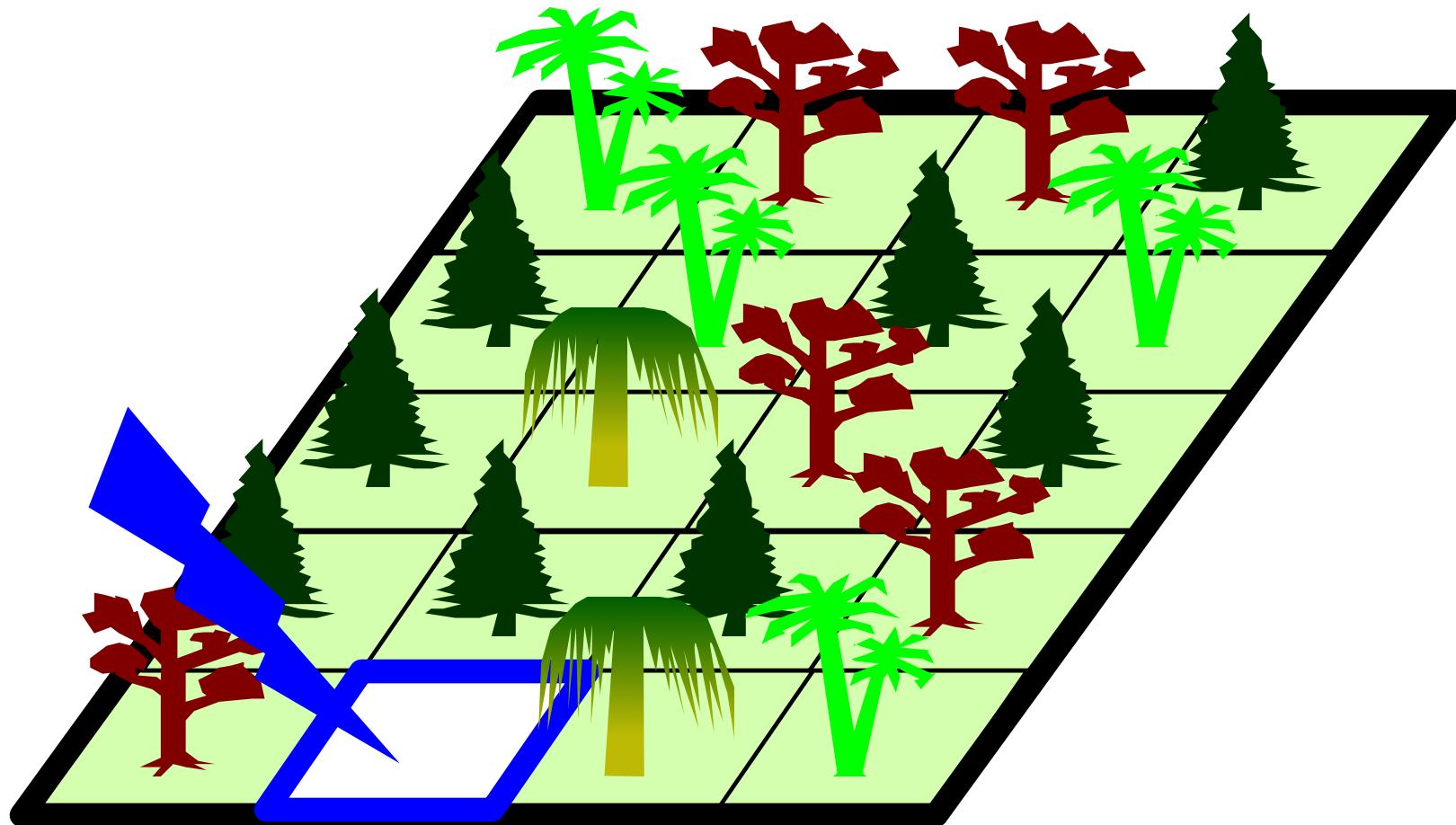
# The model rules in brief



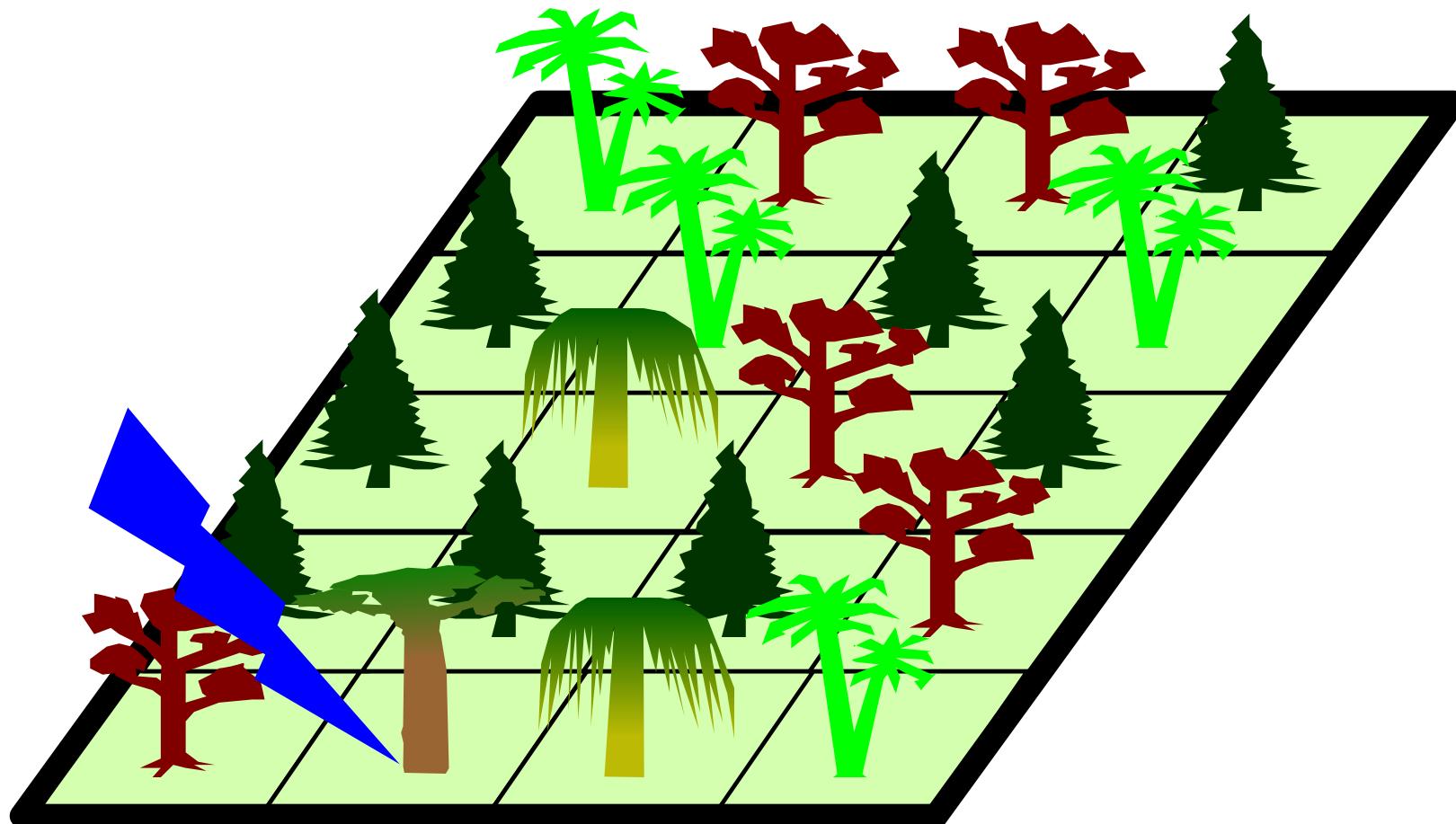
# The model rules in brief



# The model rules in brief



# The model rules in brief



# Dynamic equilibrium:

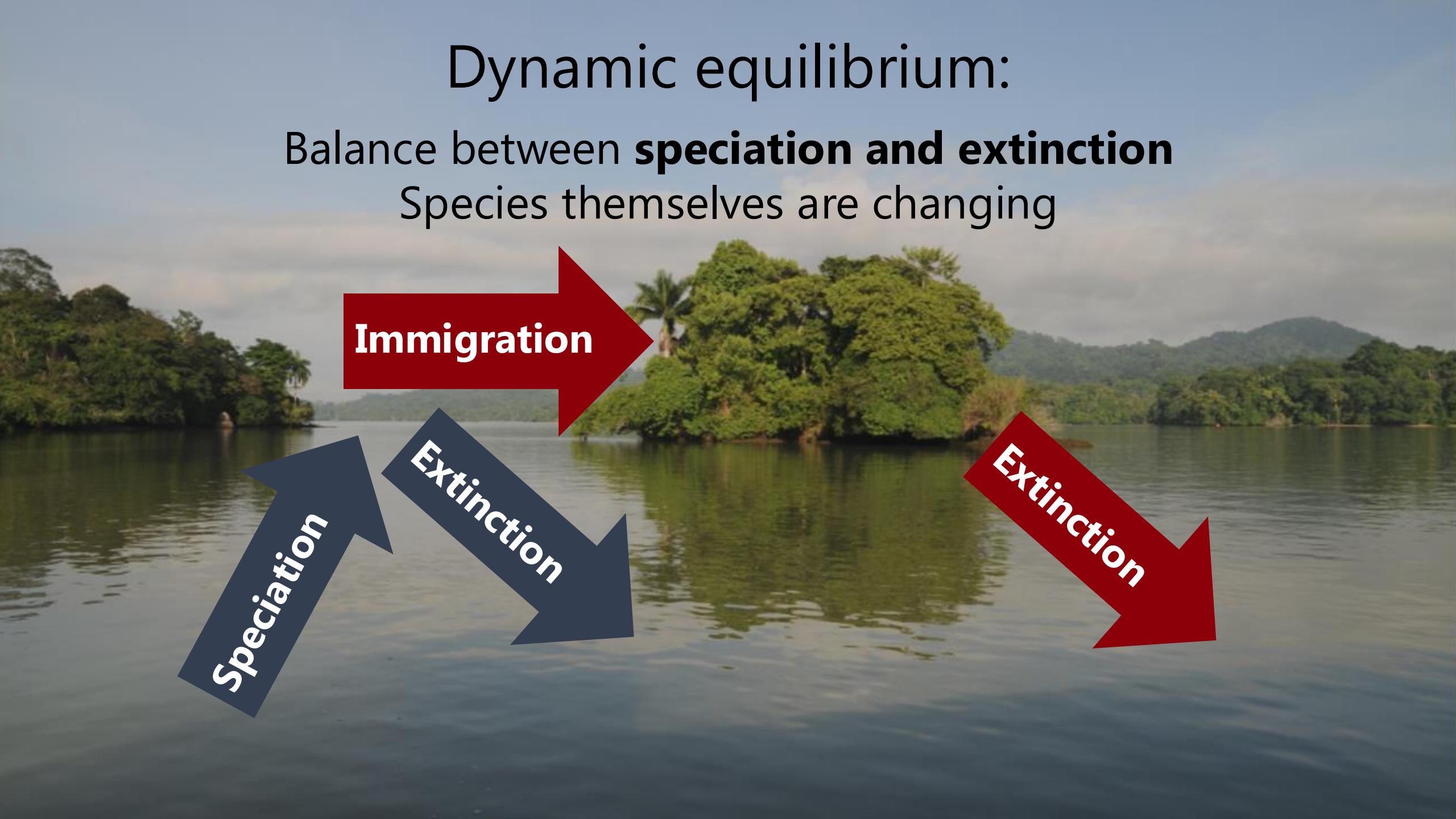
Balance between immigration and extinction  
Species themselves are changing



Immigration



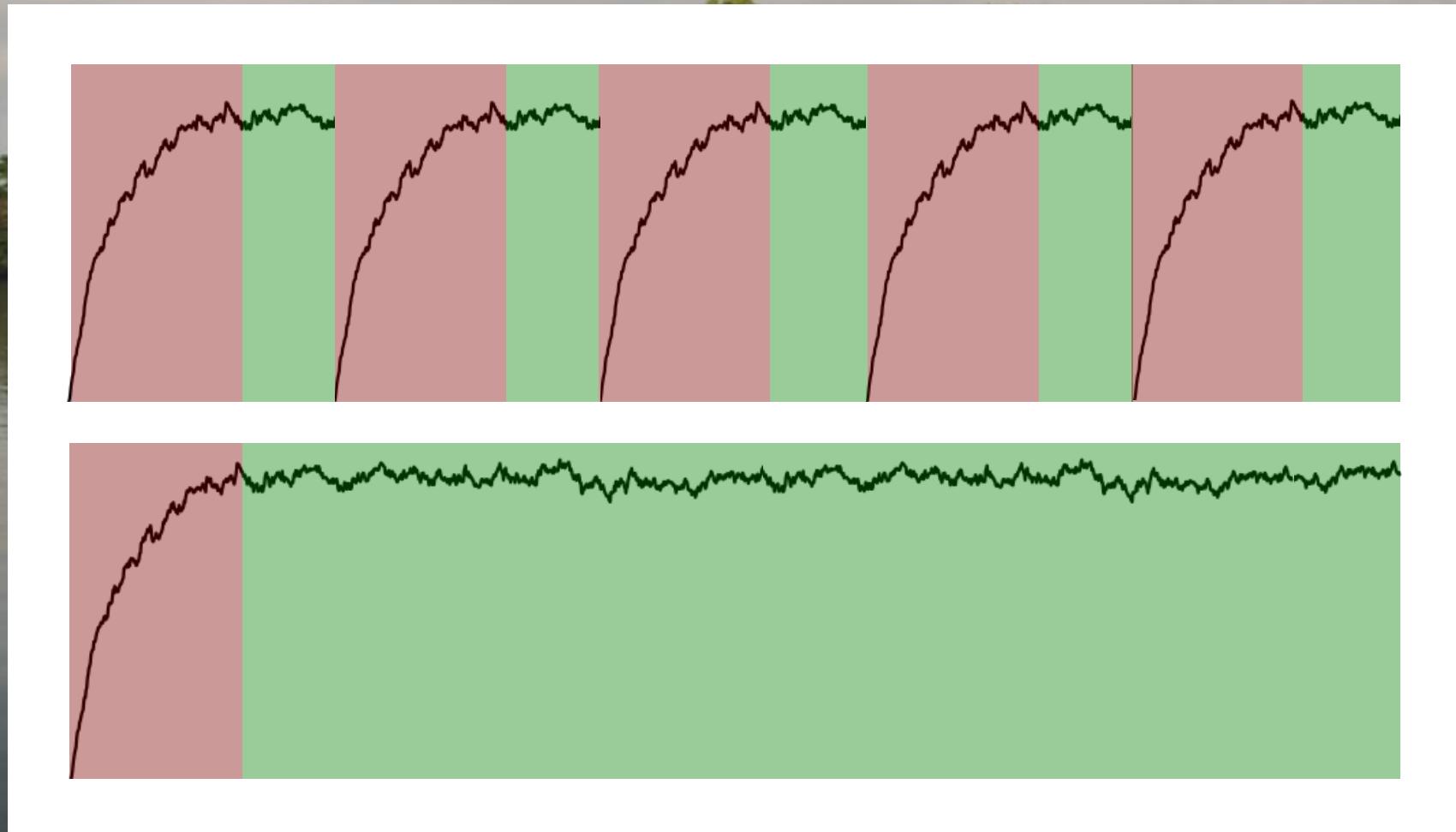
Extinction



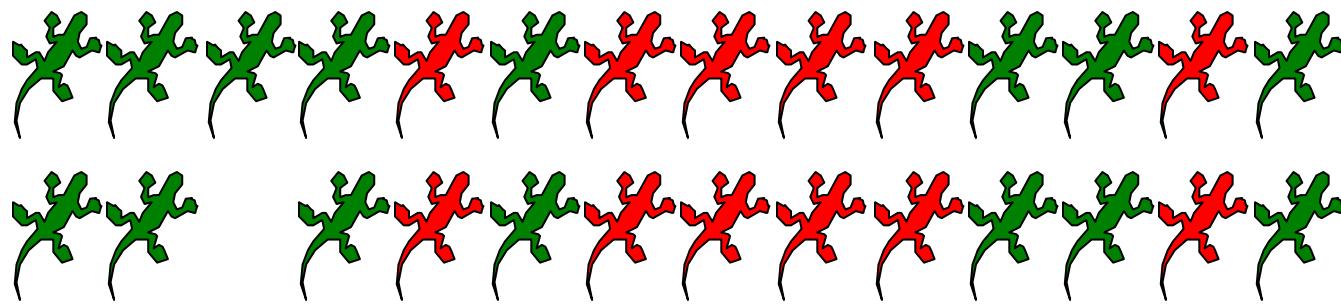
Dynamic equilibrium:  
Balance between **speciation and extinction**  
Species themselves are changing

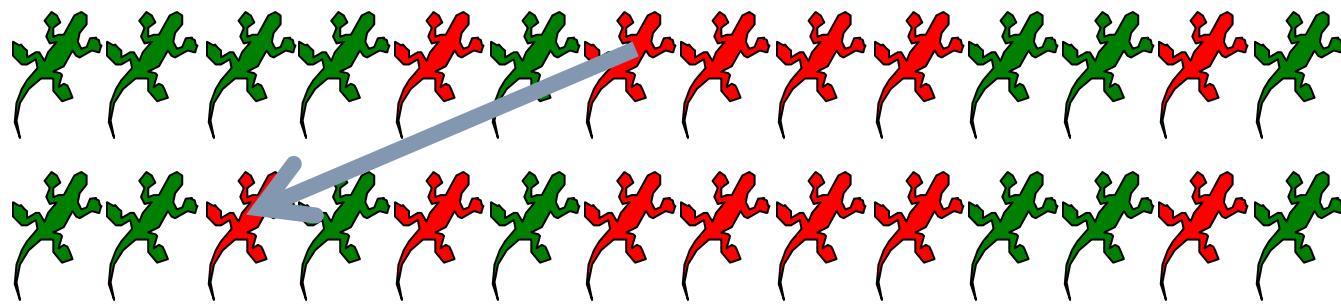


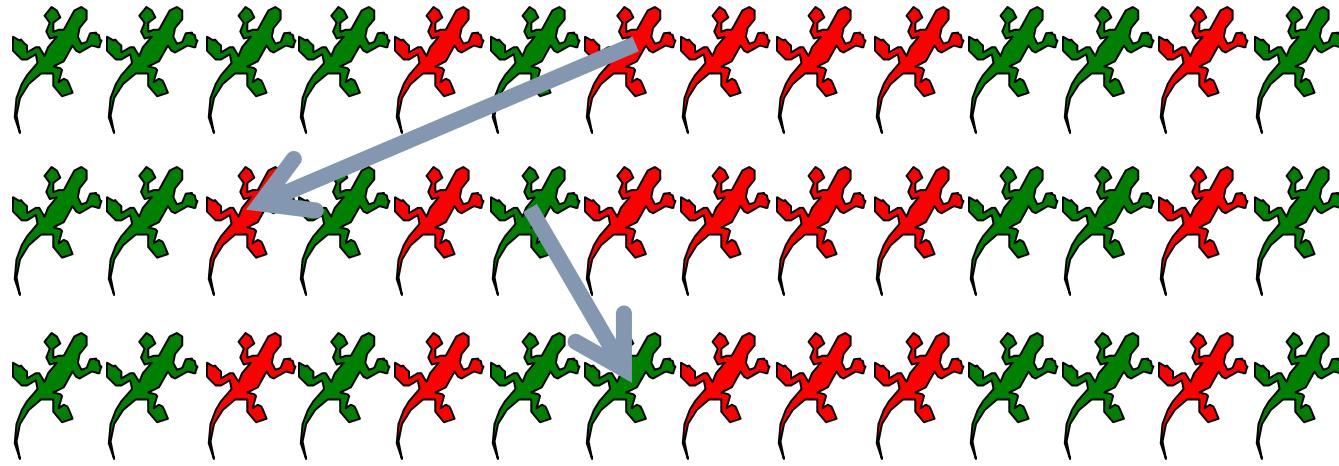
Dynamic equilibrium:  
Balance between **speciation and extinction**  
Species themselves are changing

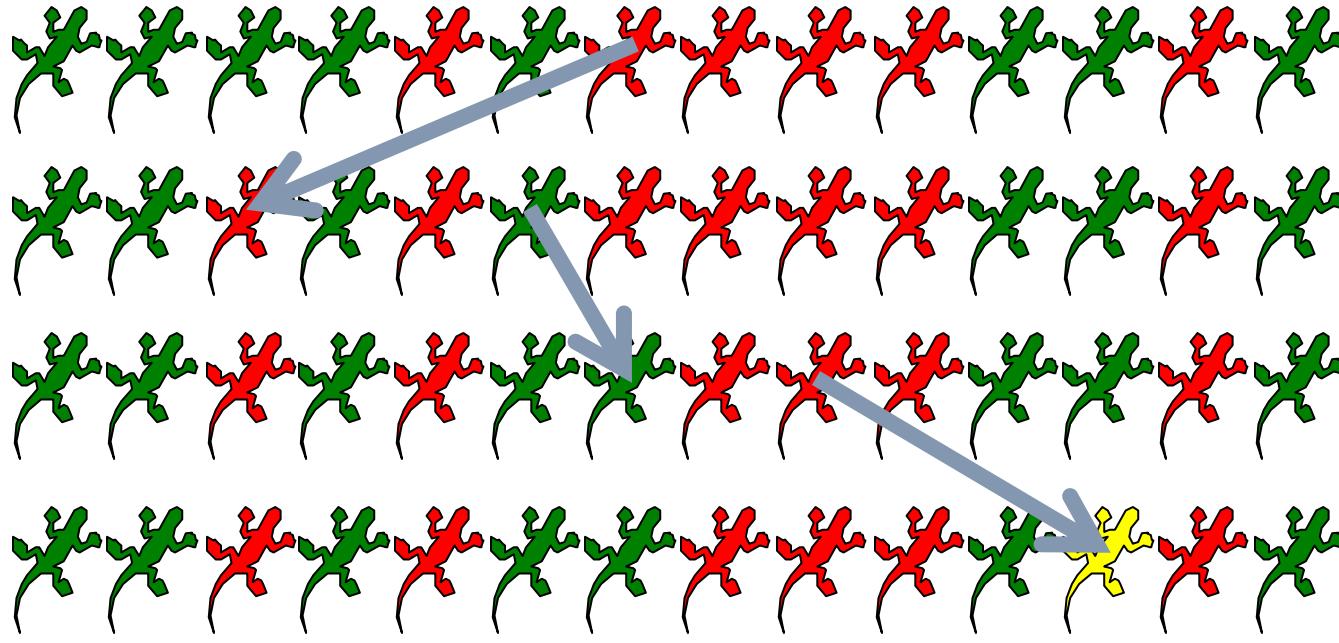


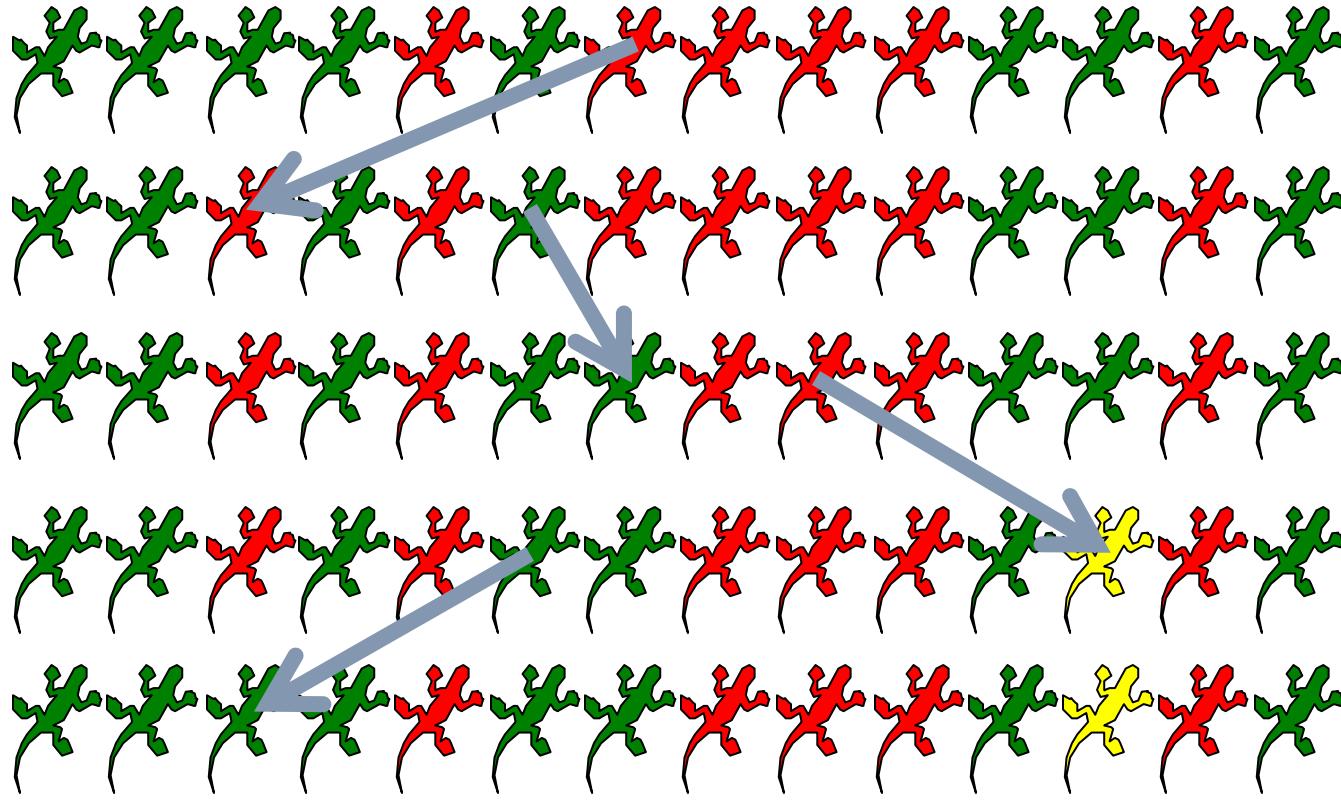


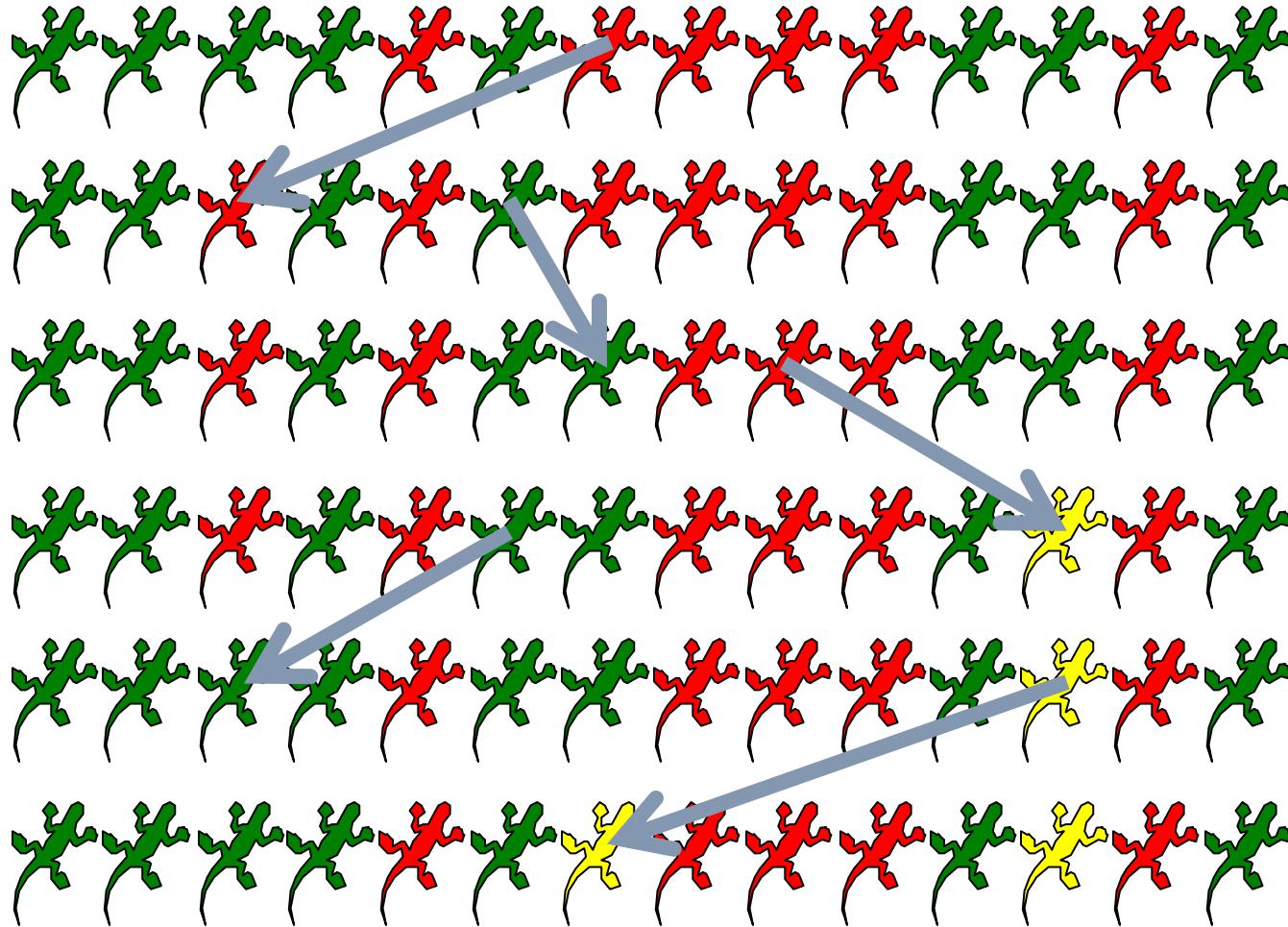


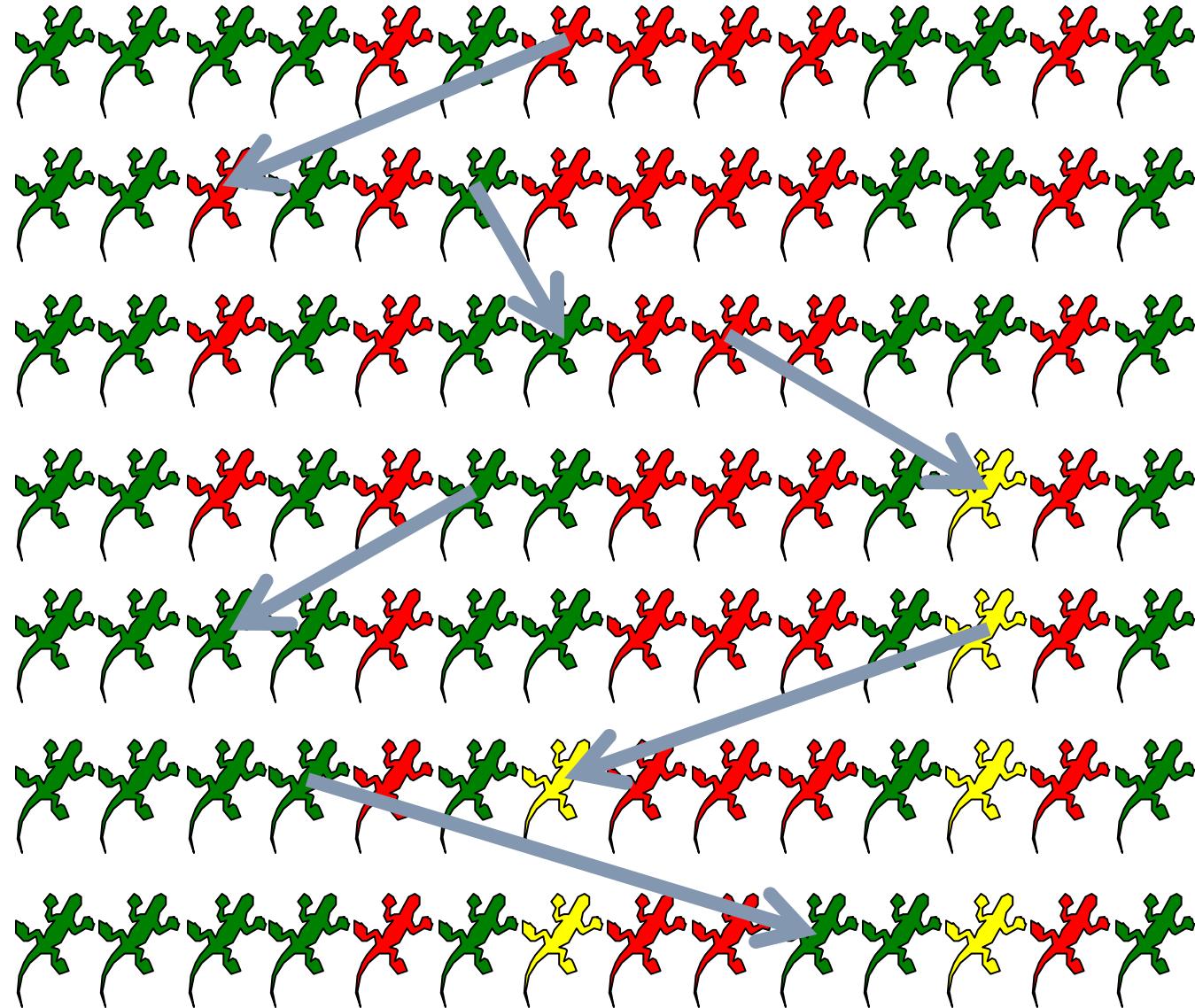


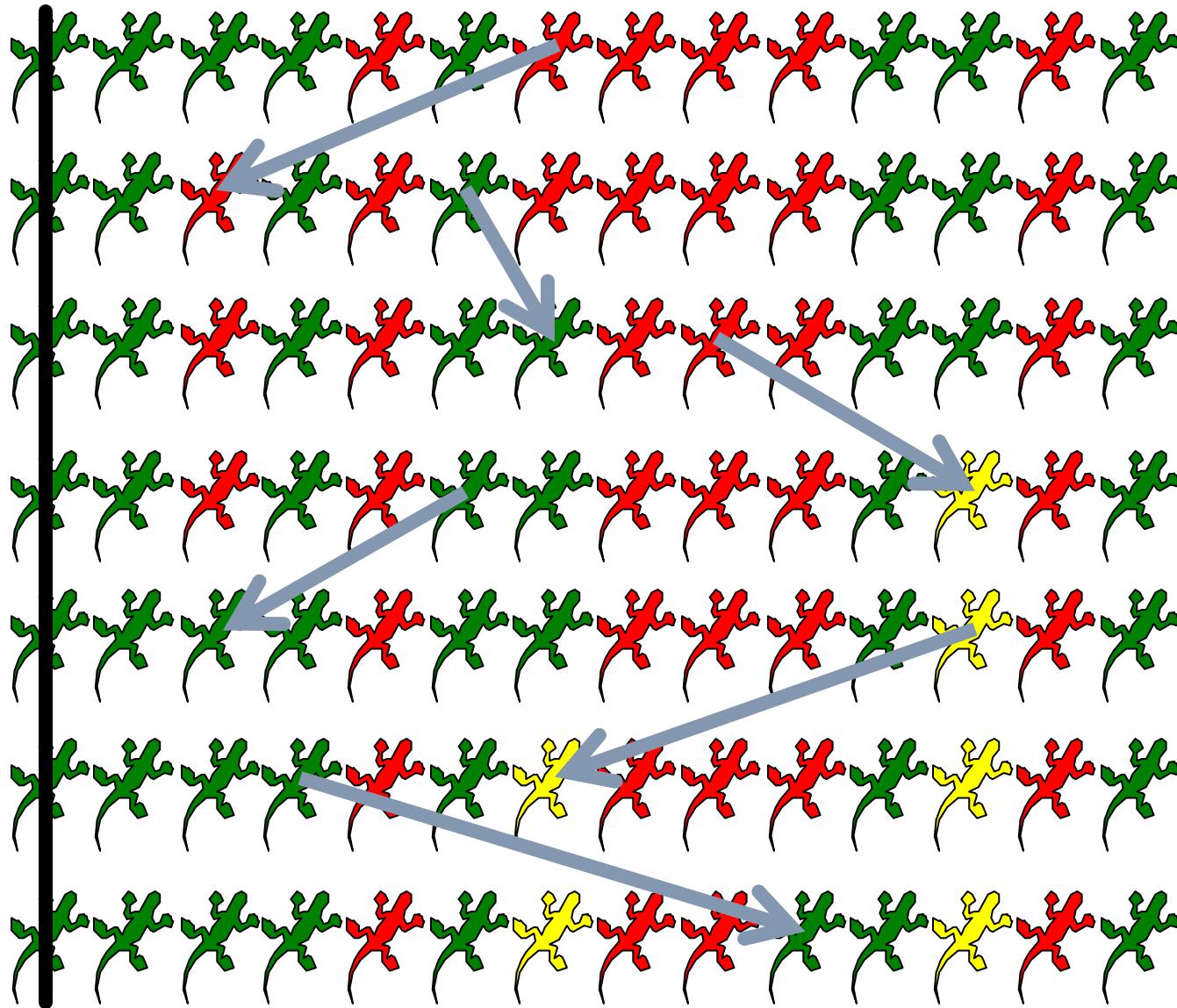


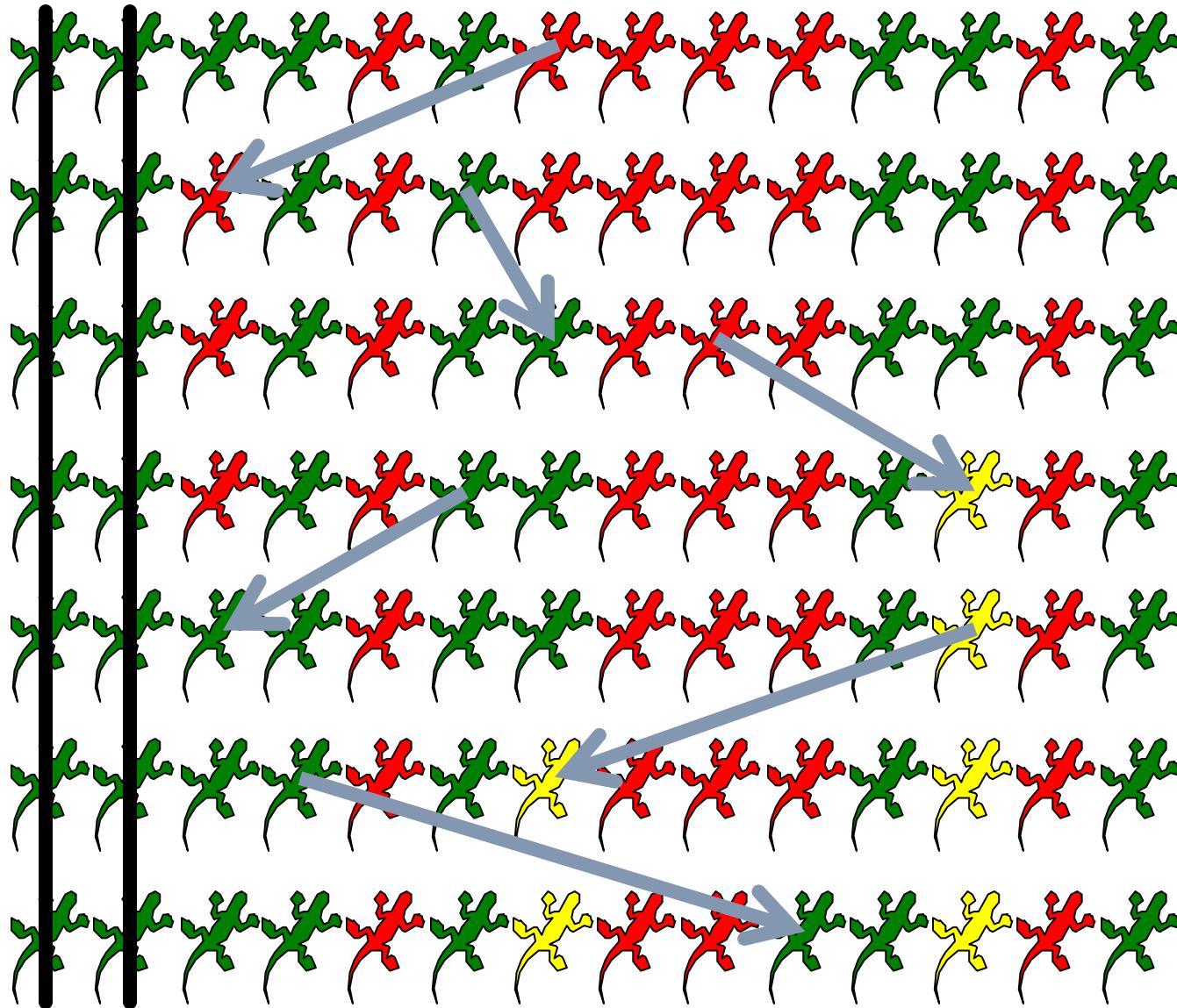


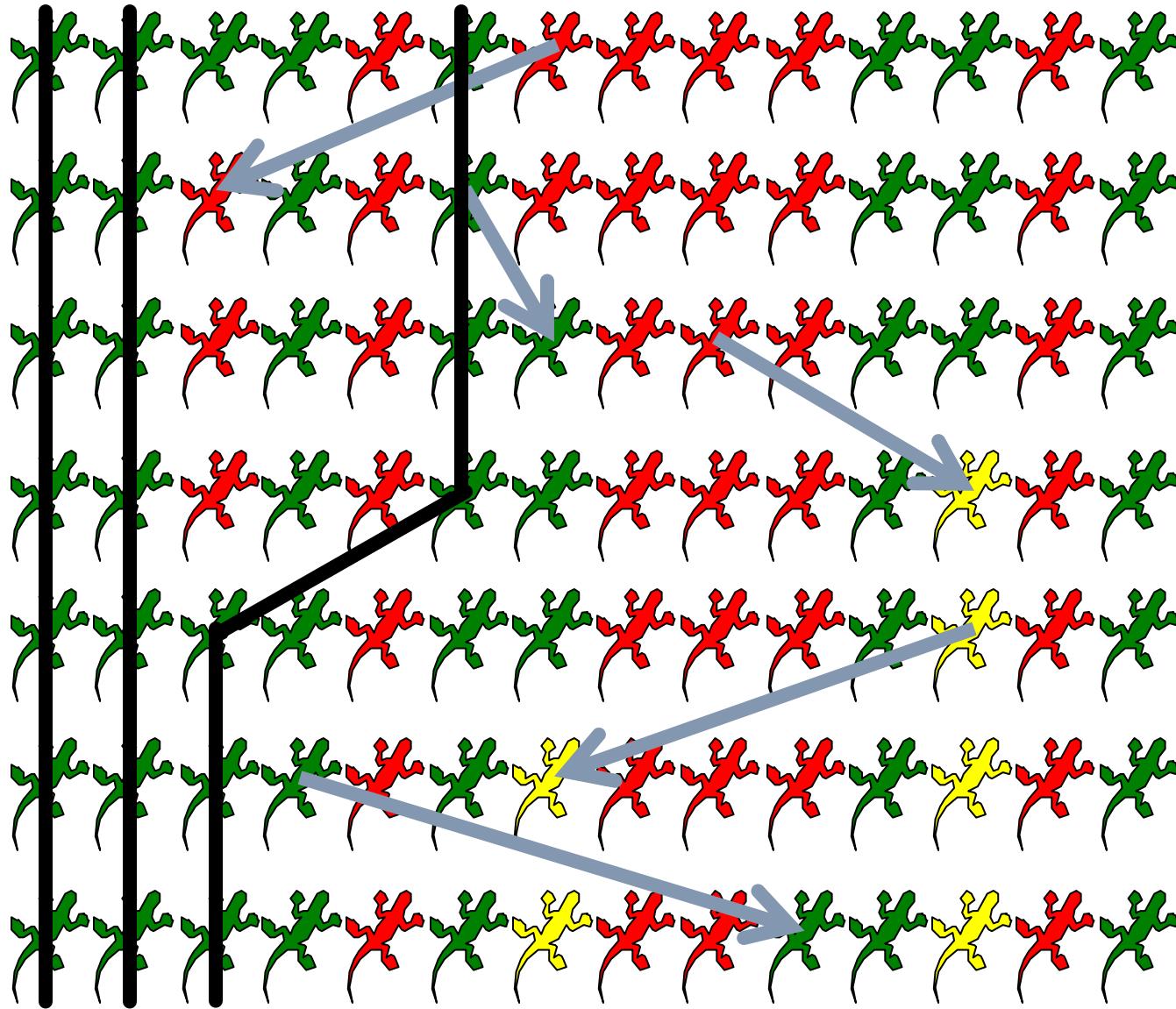


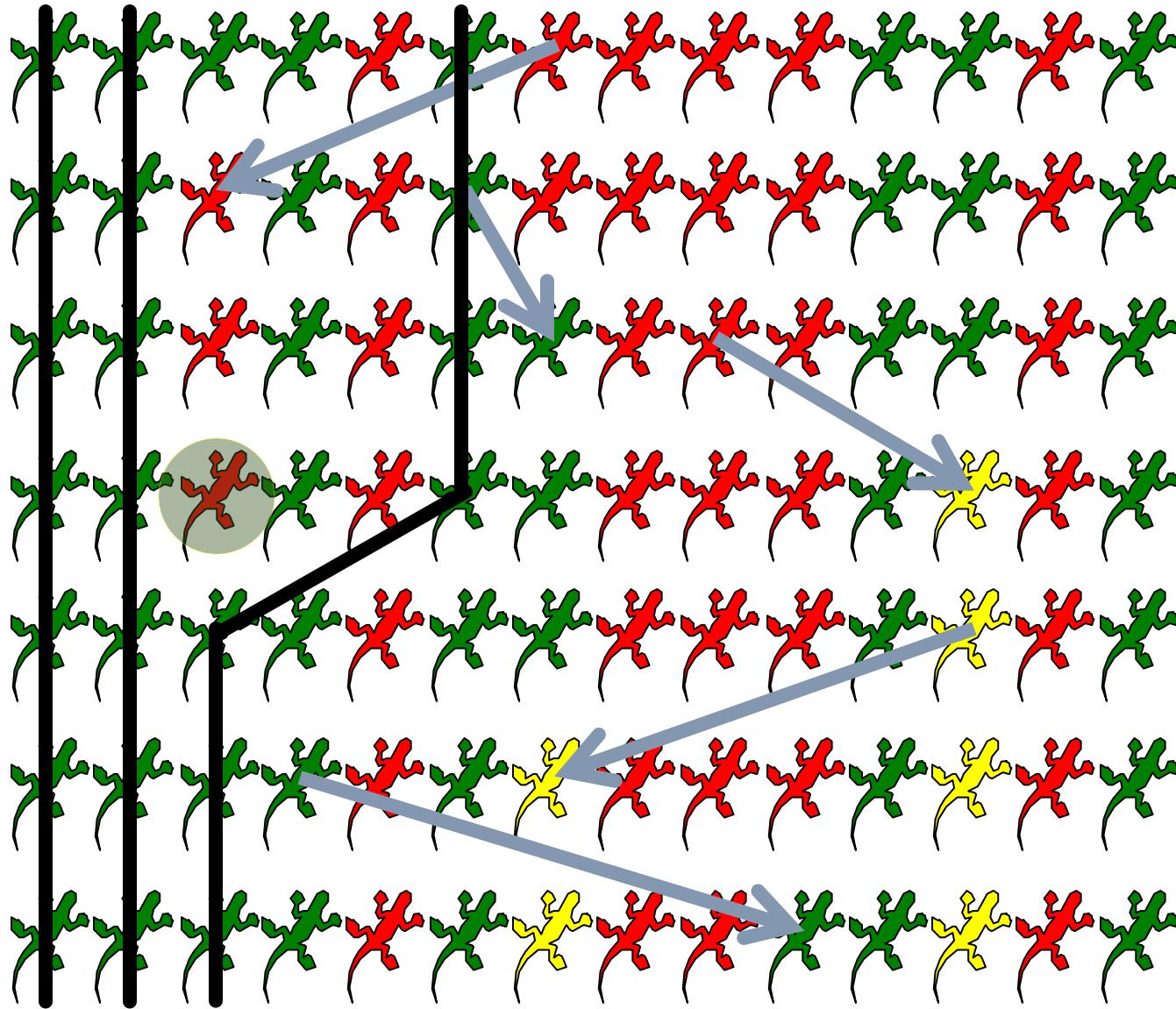


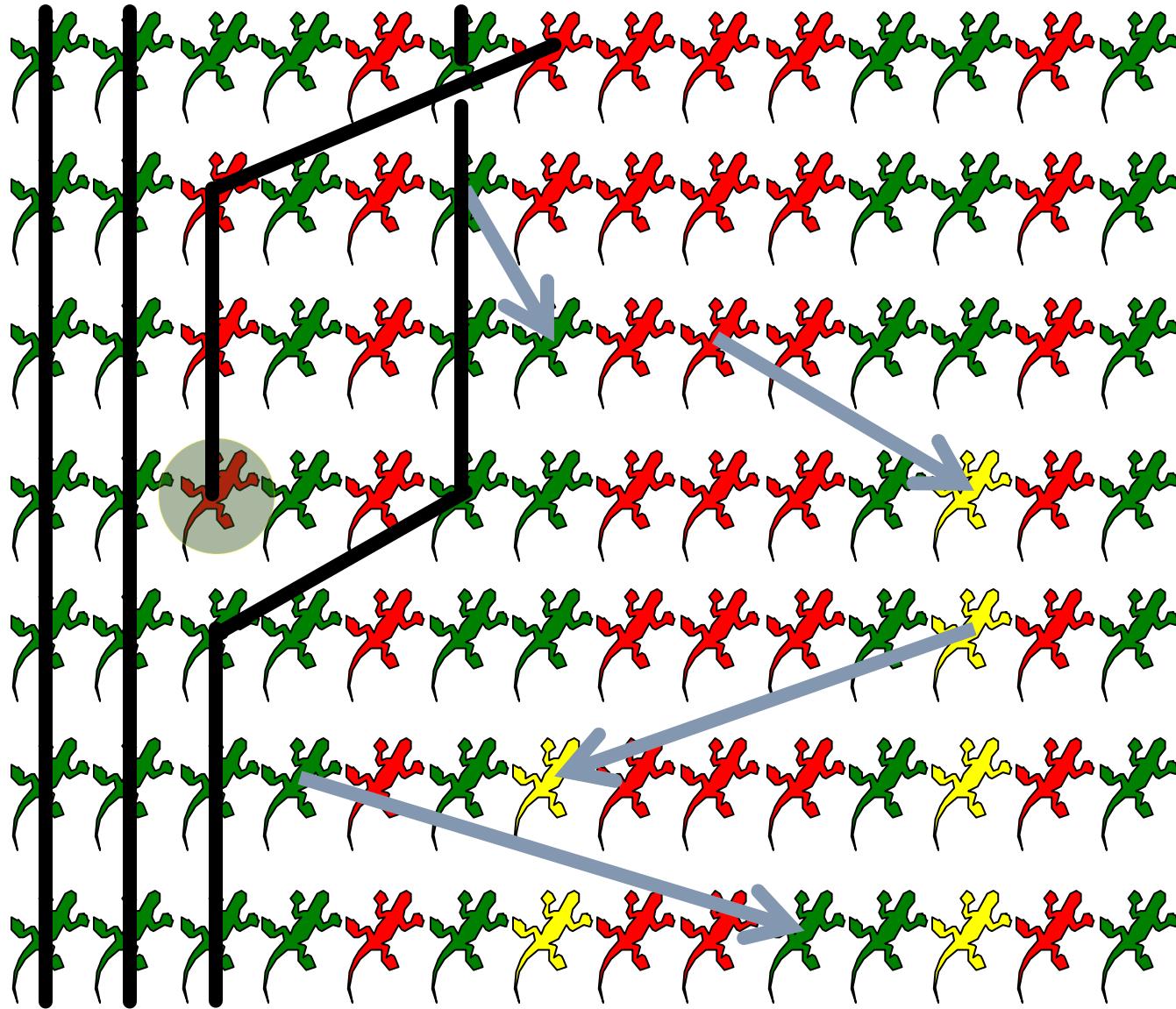


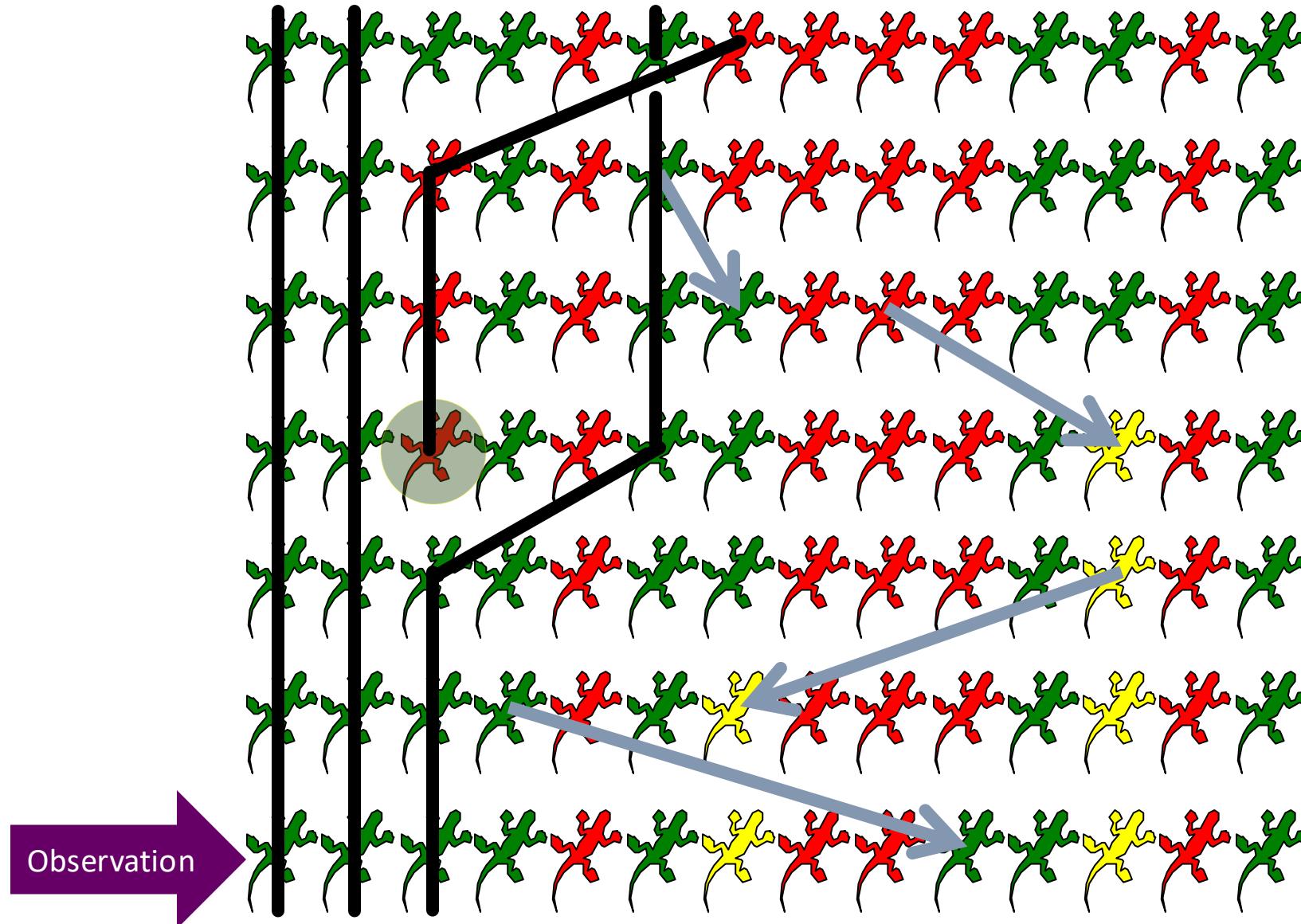


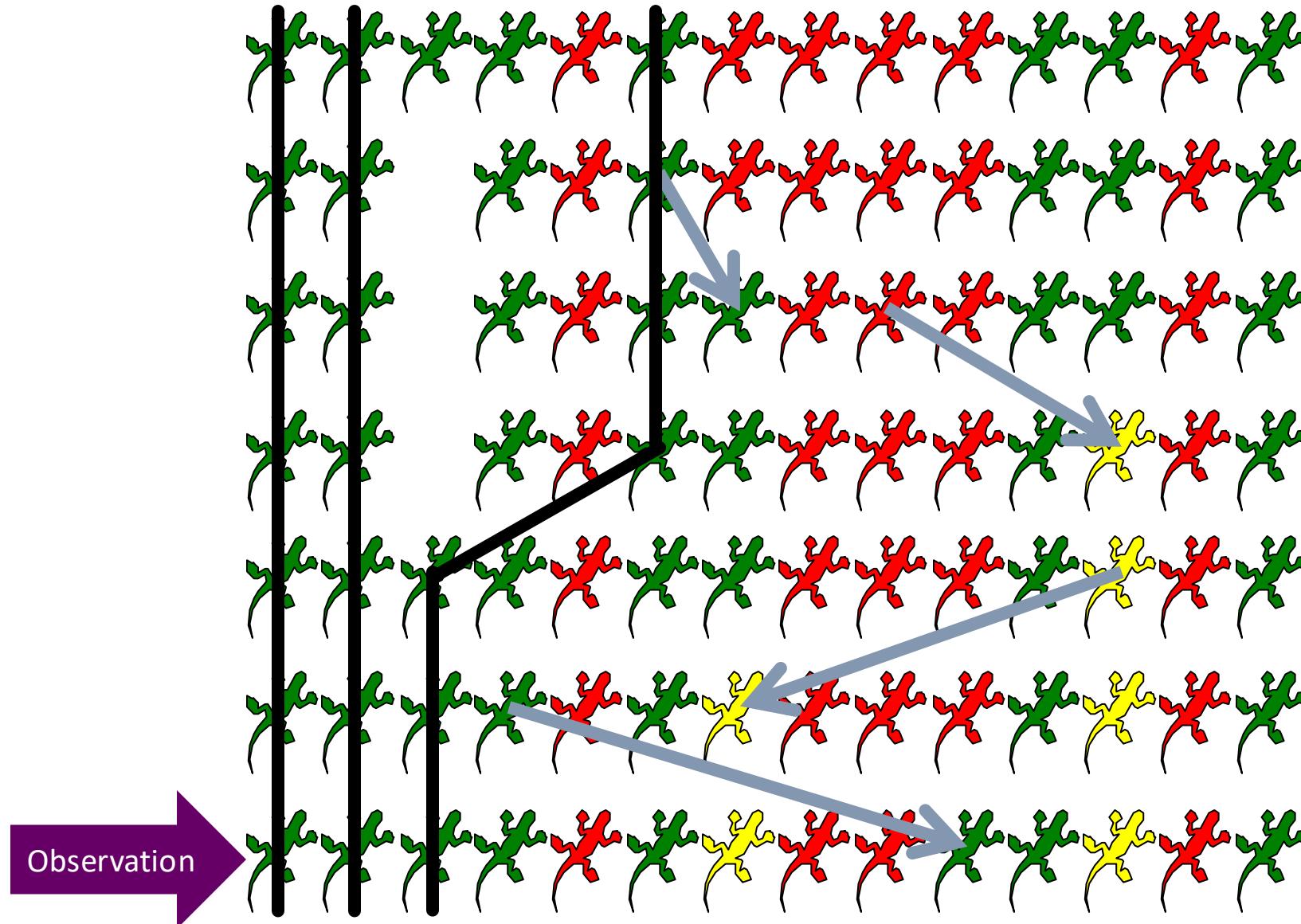


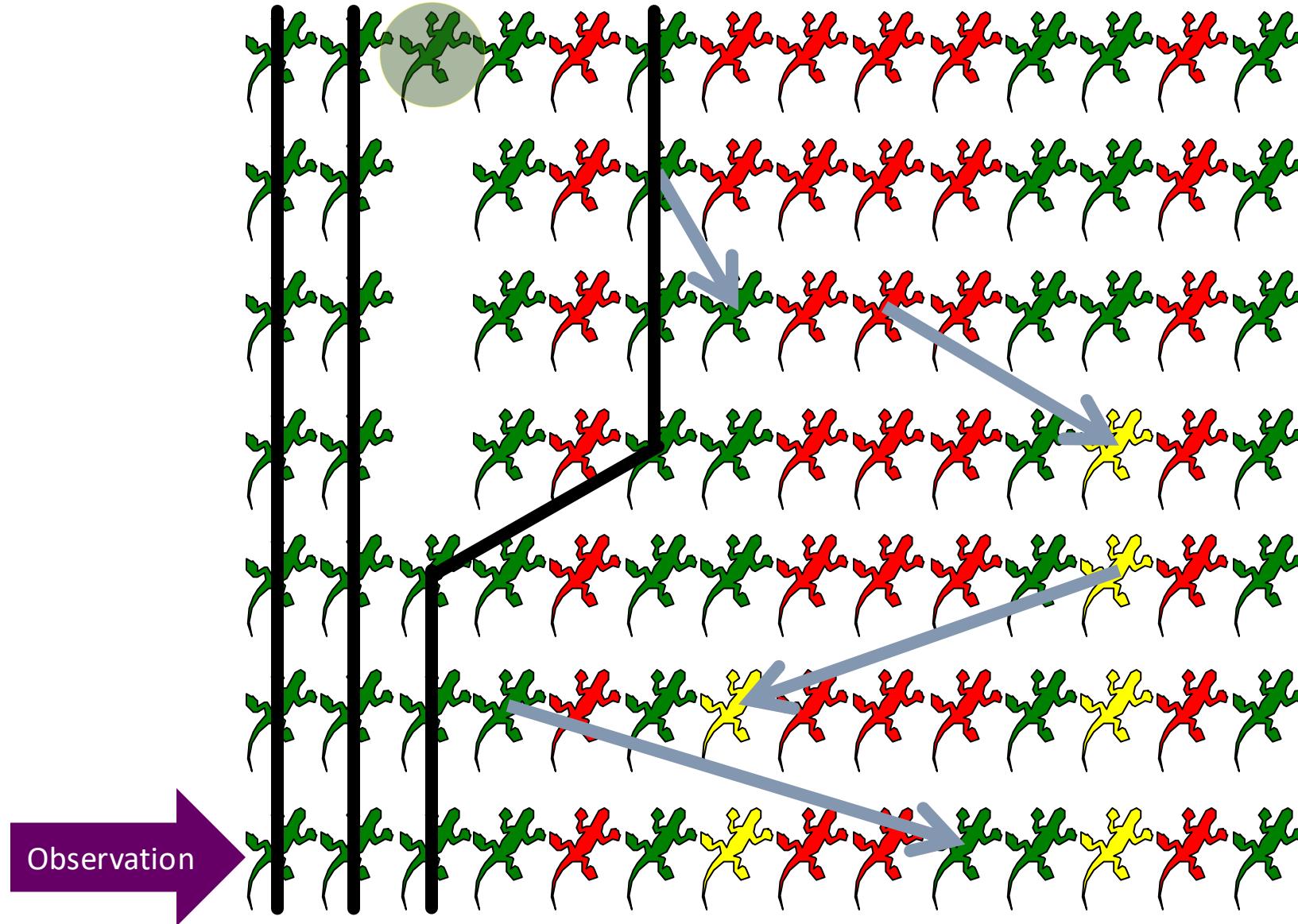


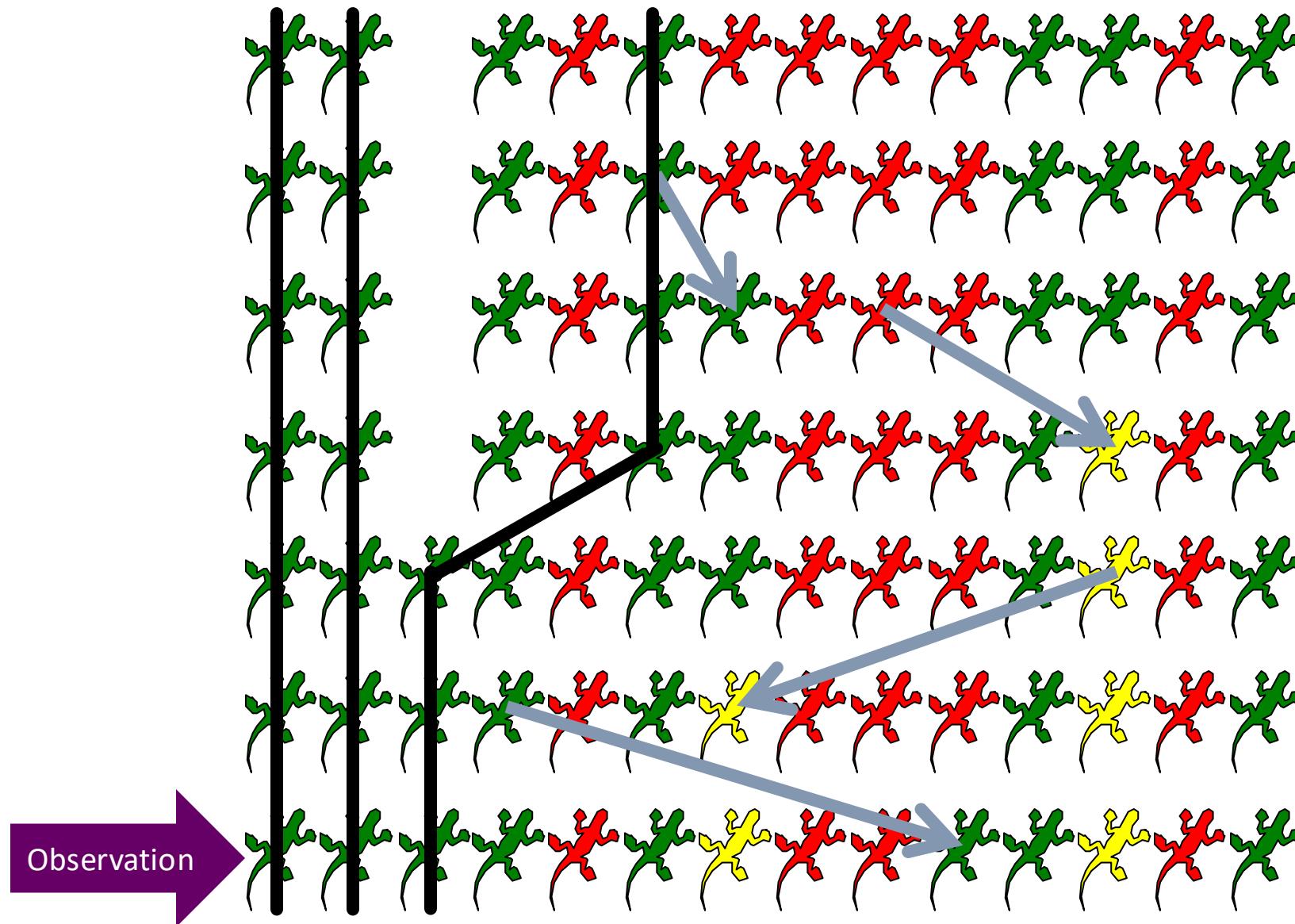


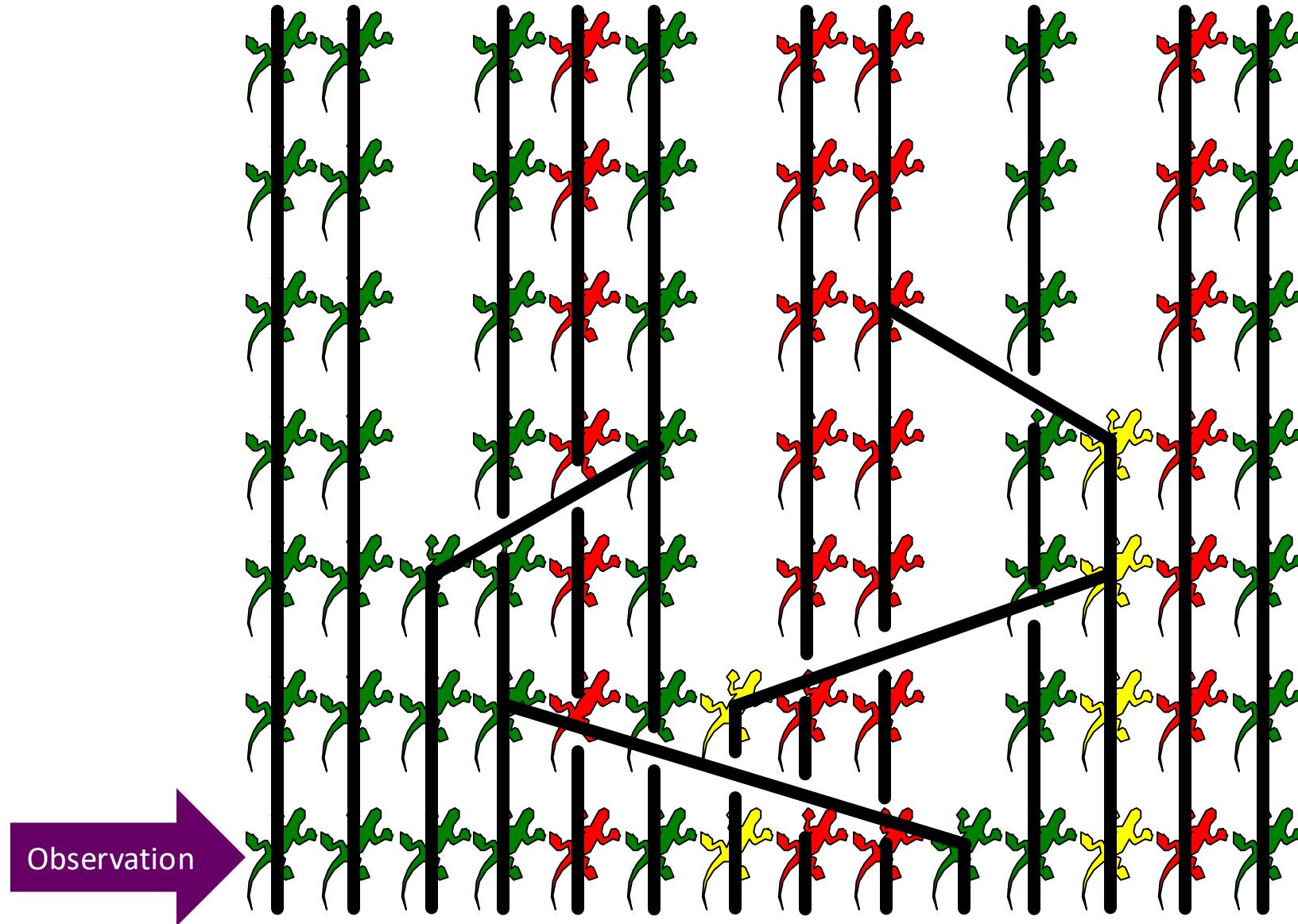


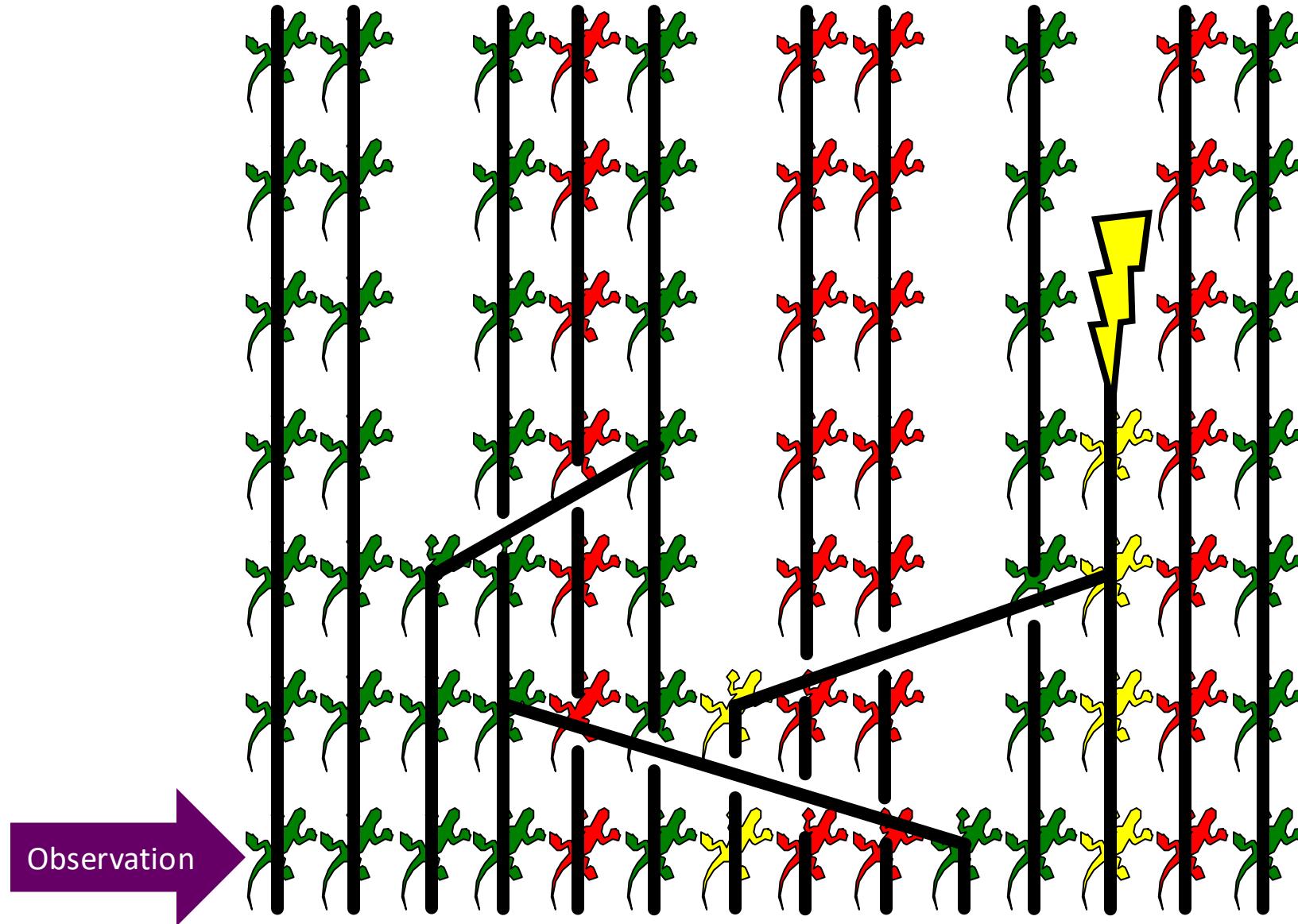


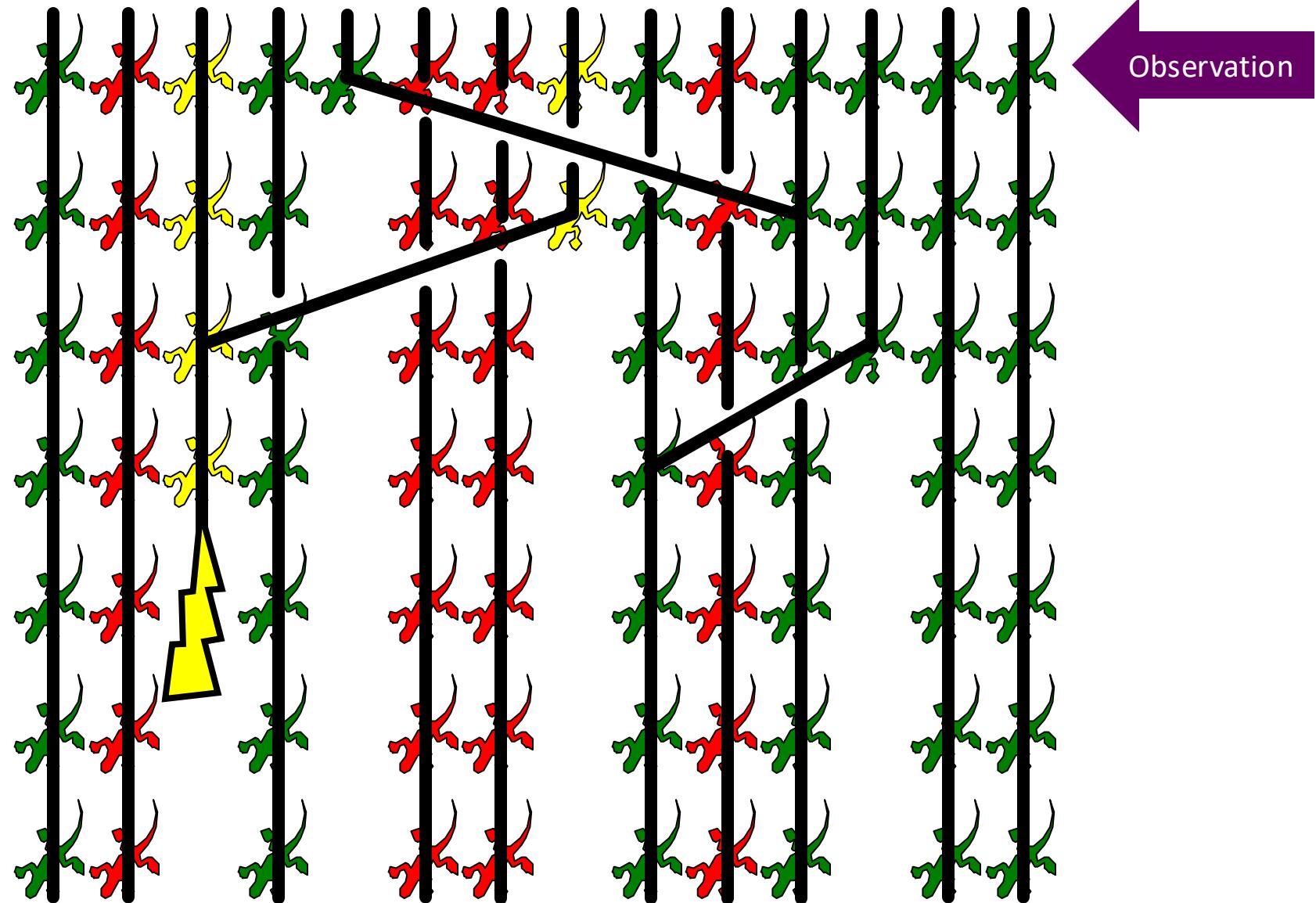


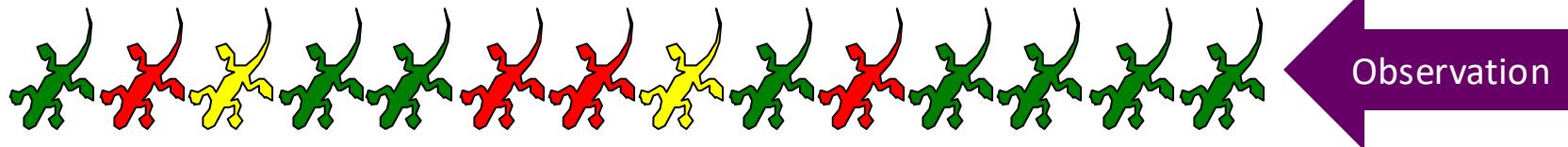




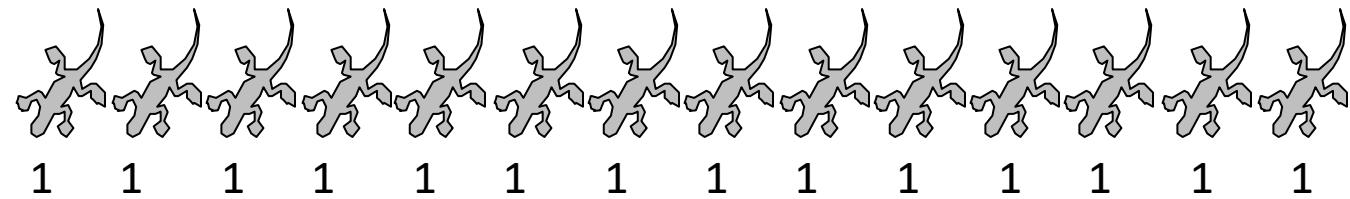




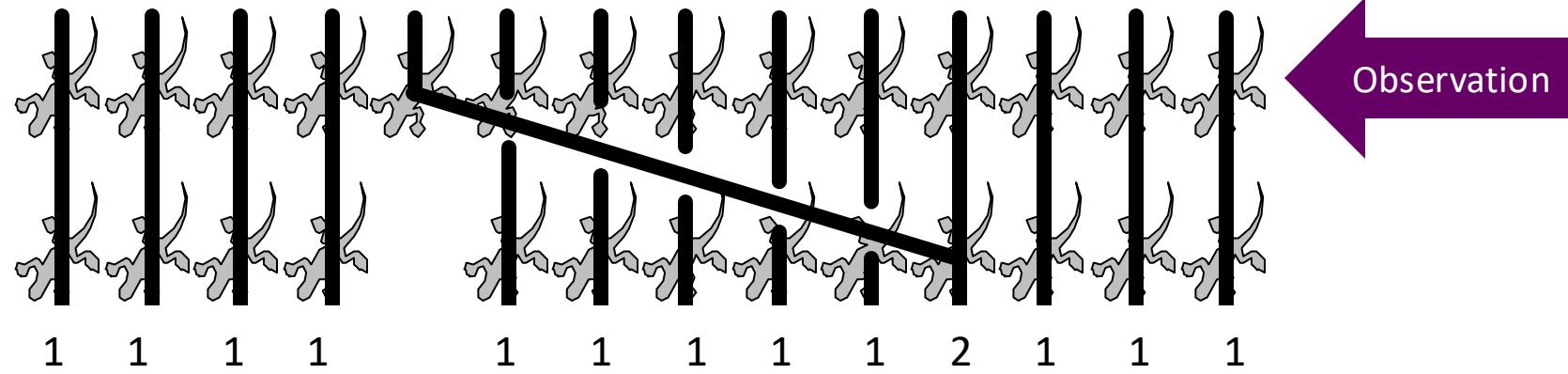


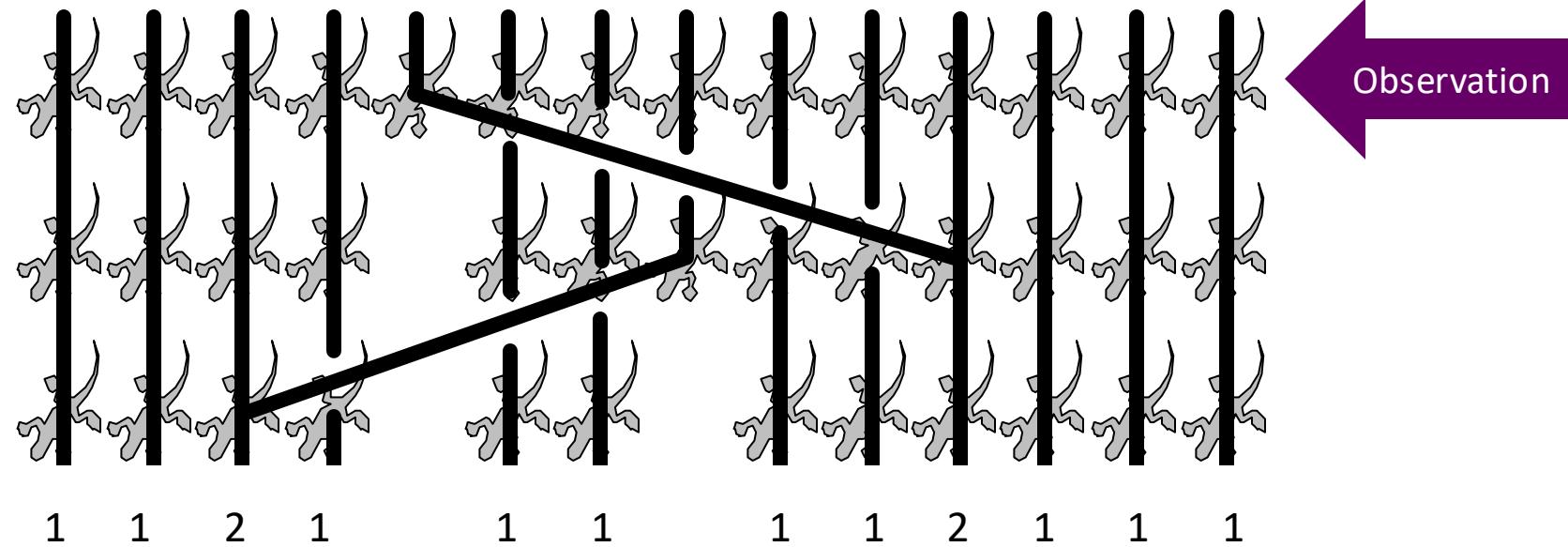


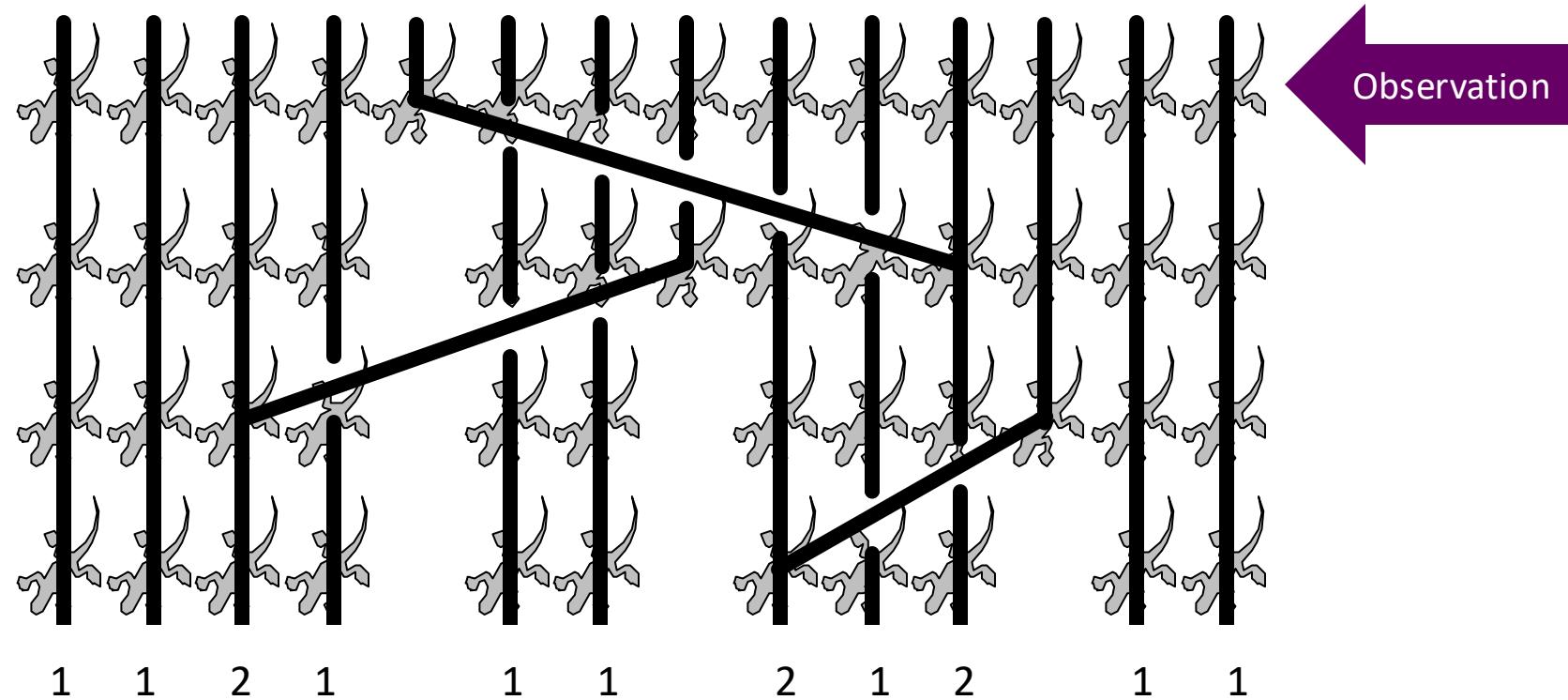
Observation

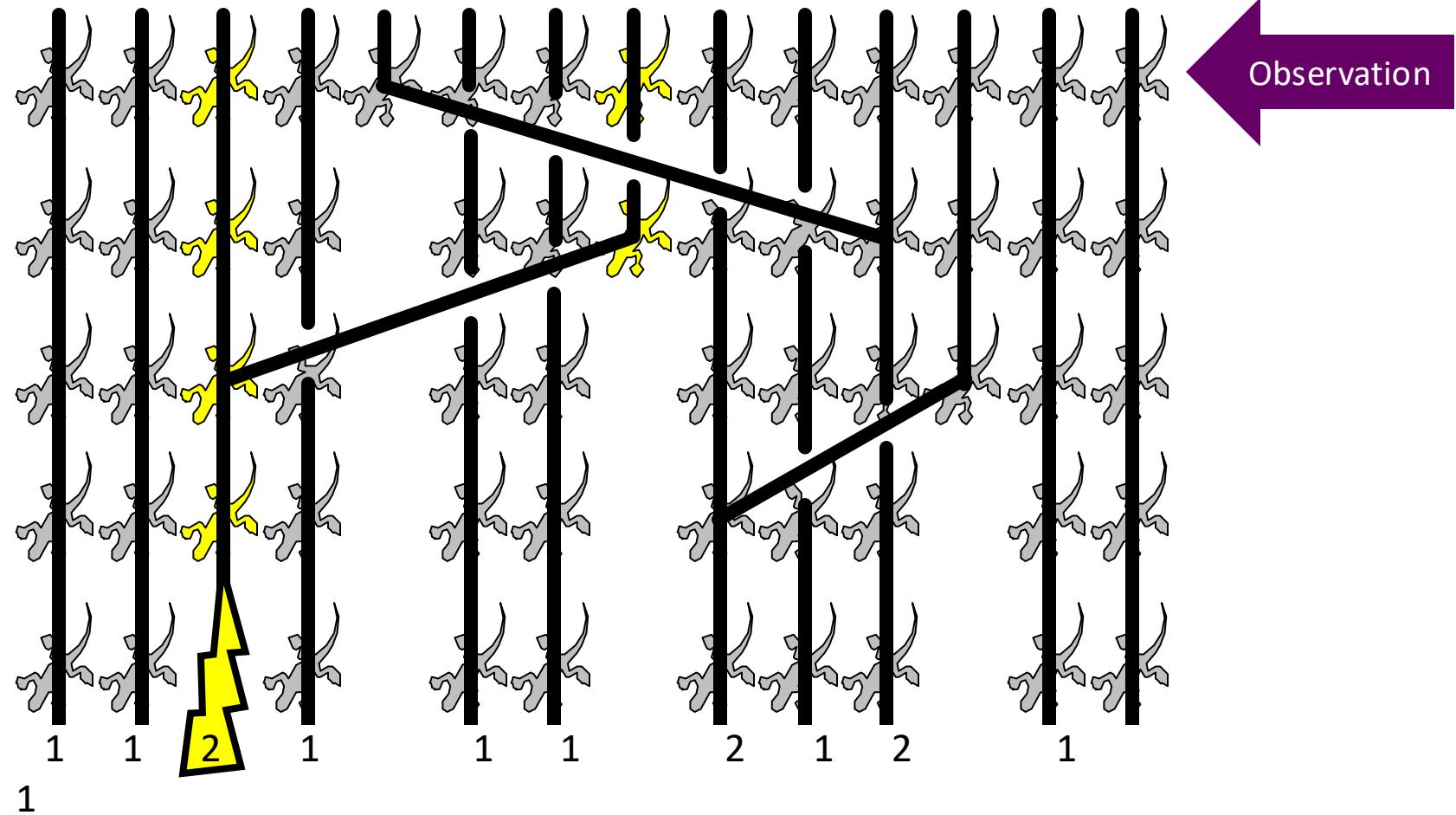


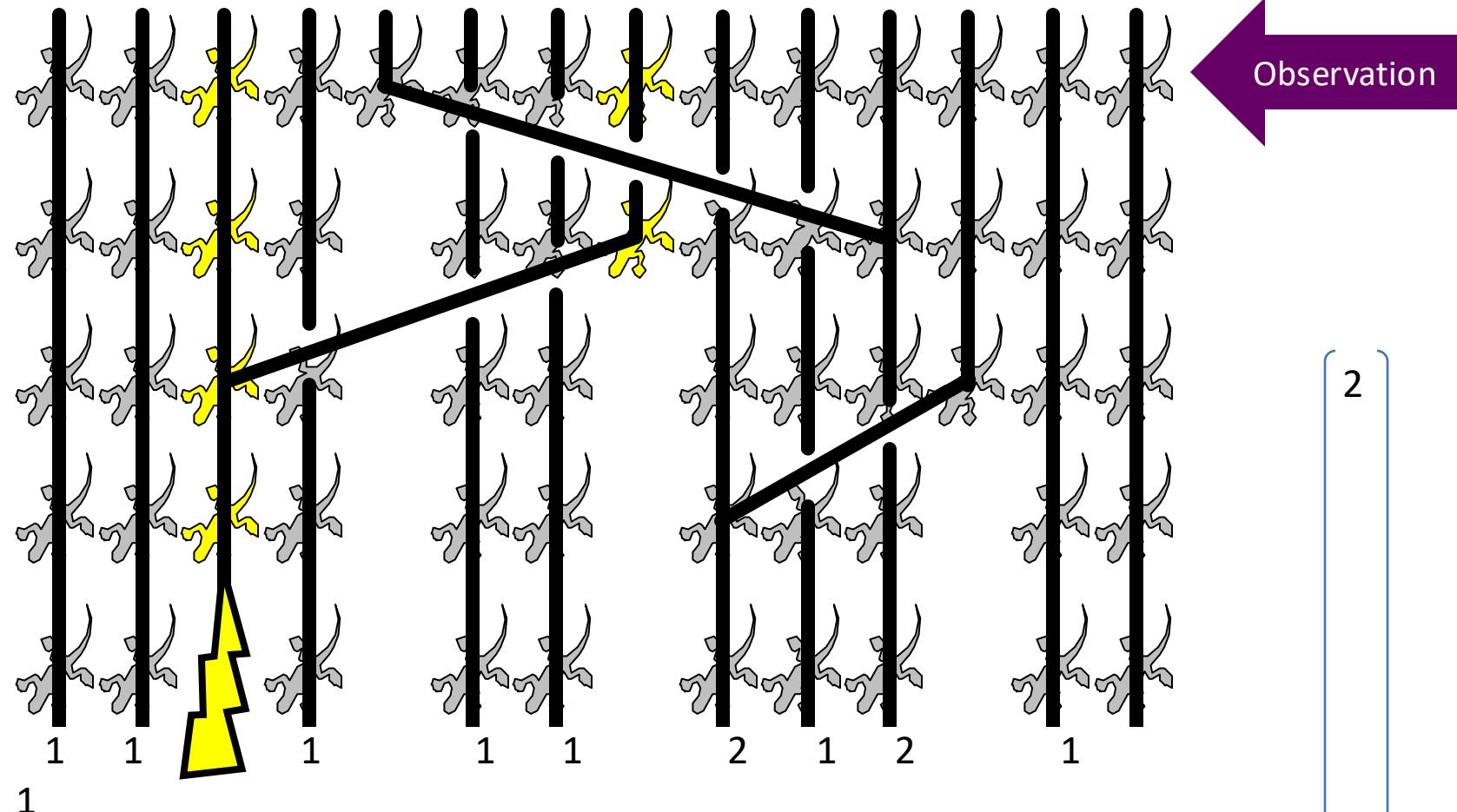
Observation

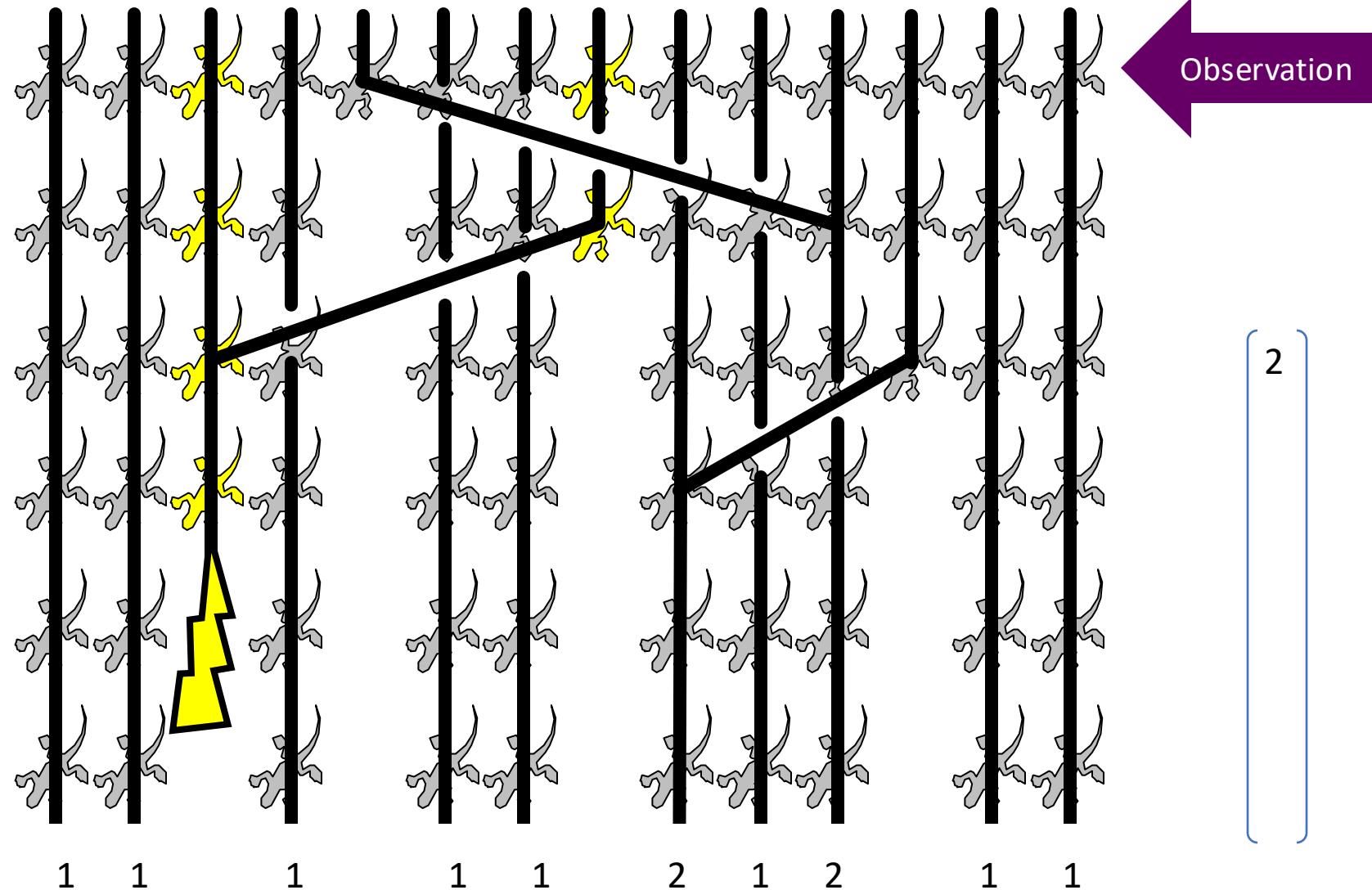


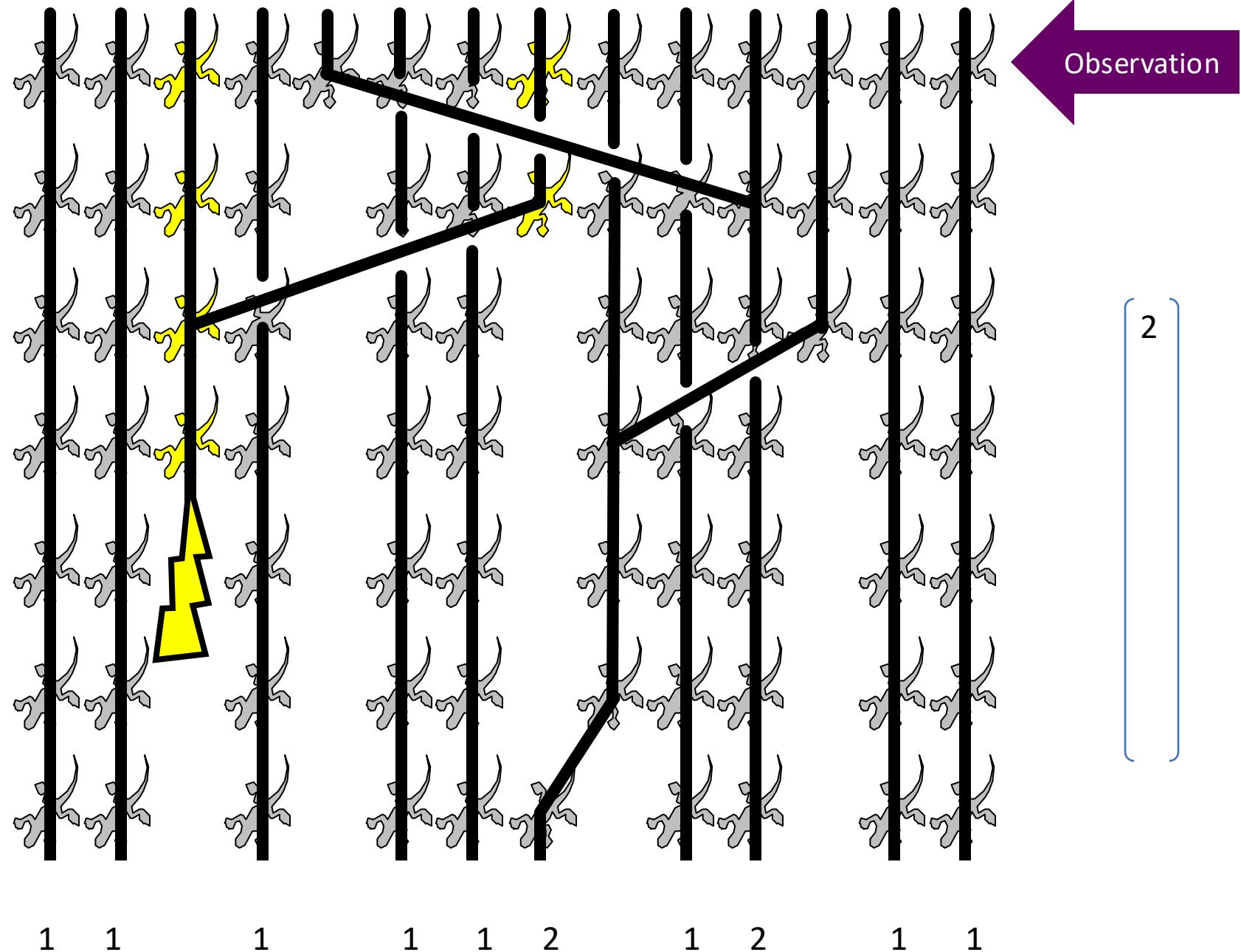


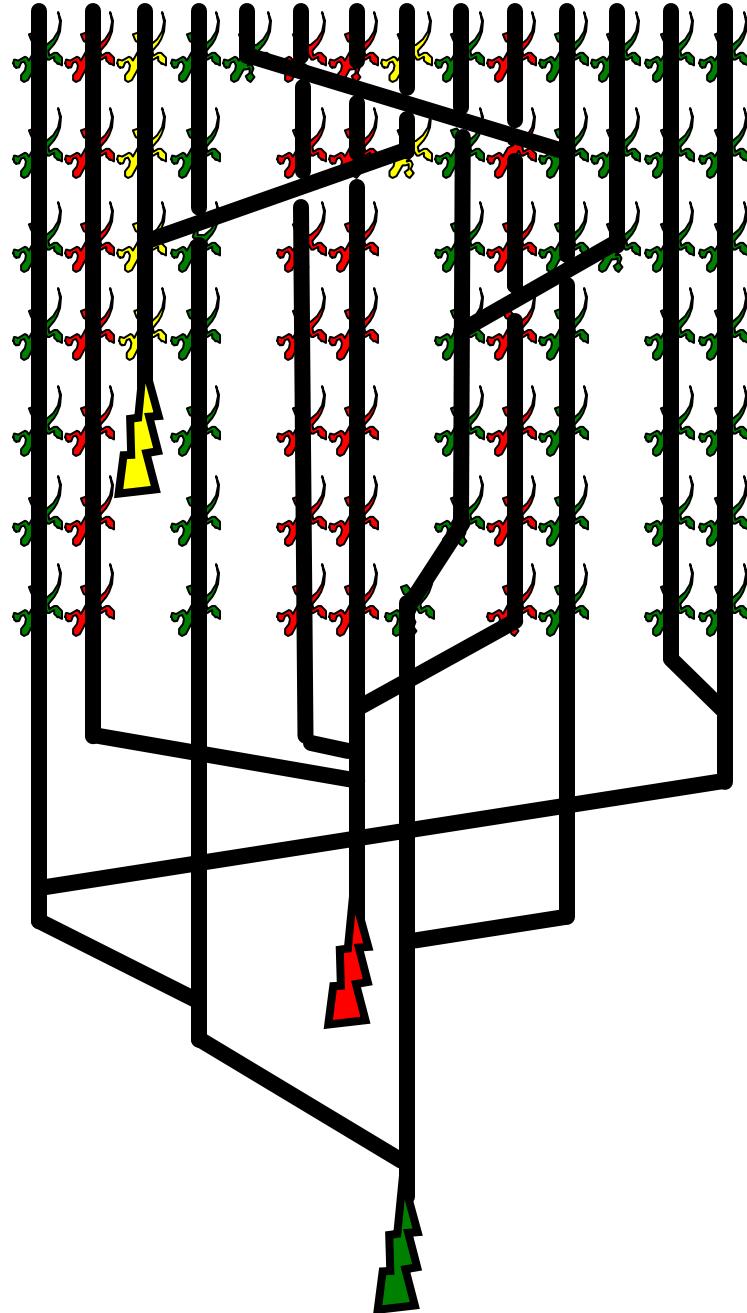






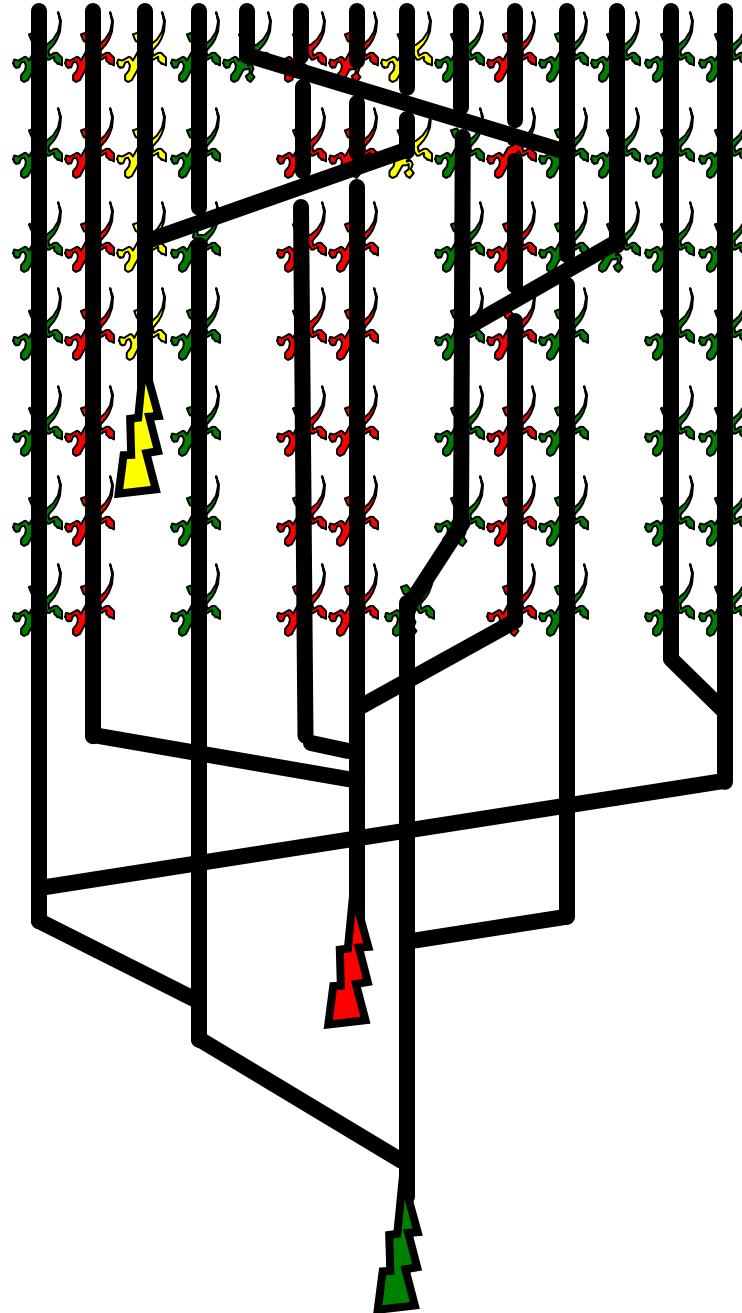






Observation

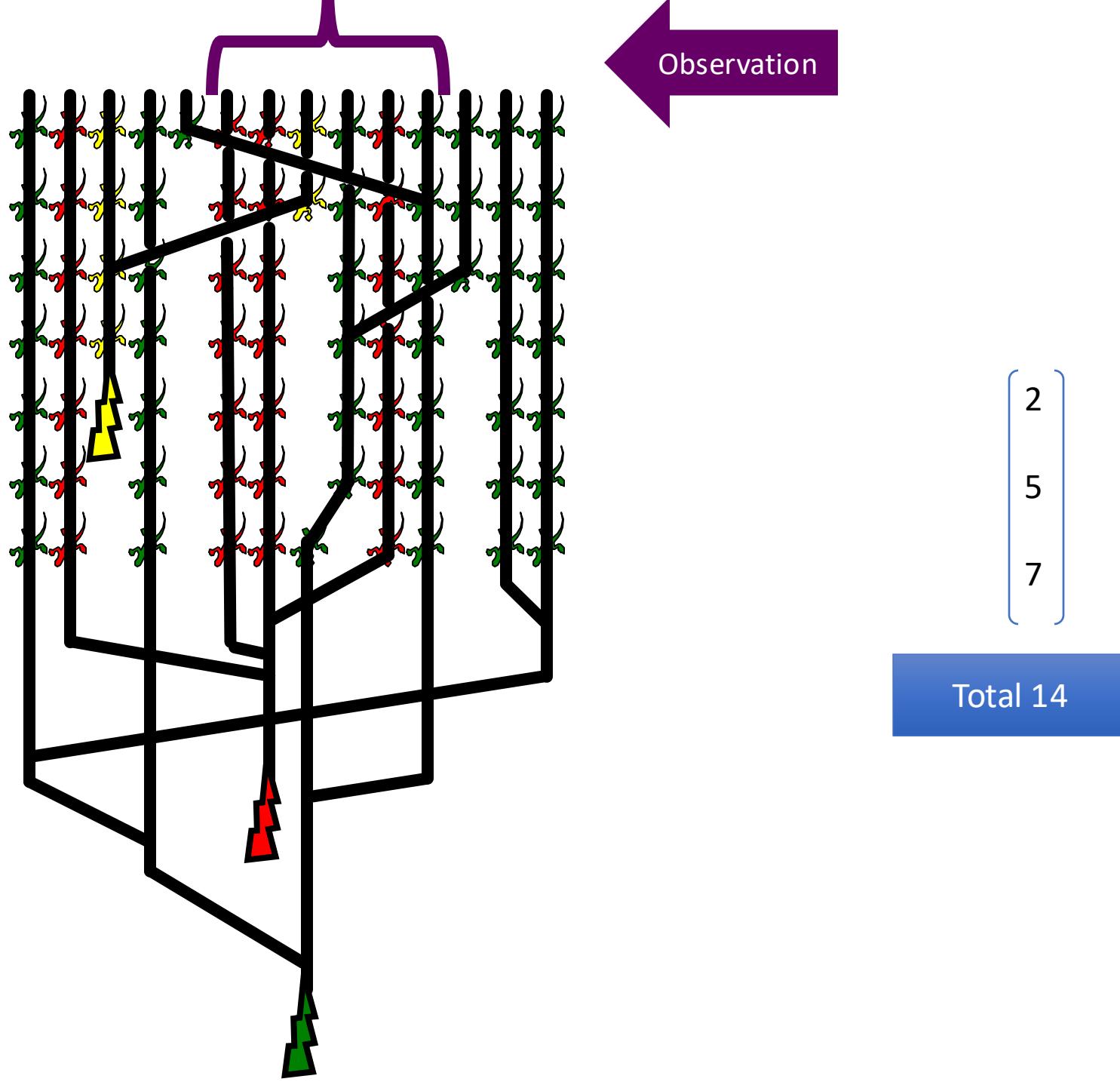
[  
2  
4  
8

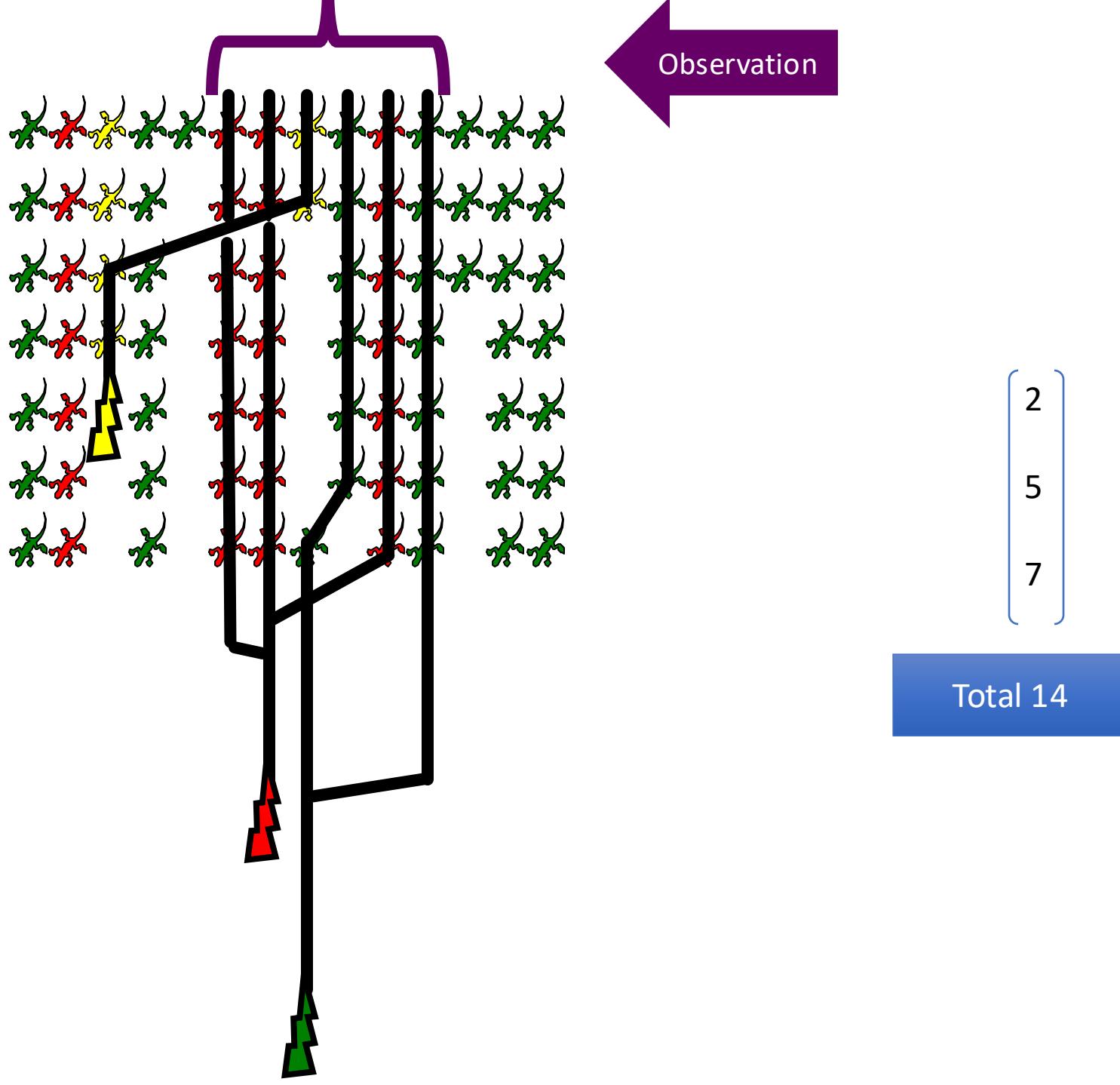


Observation

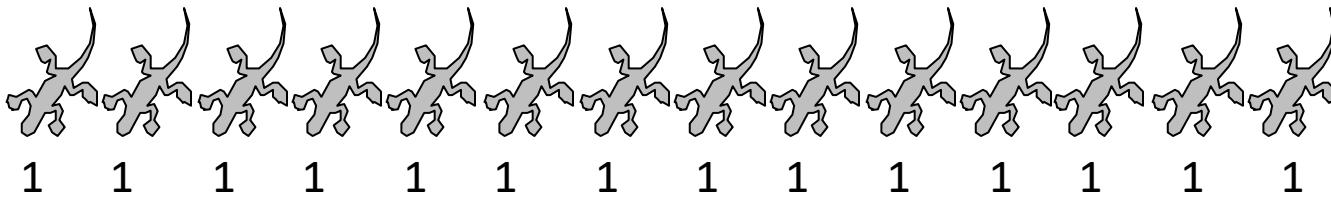
[  
2  
5  
7

Total 14



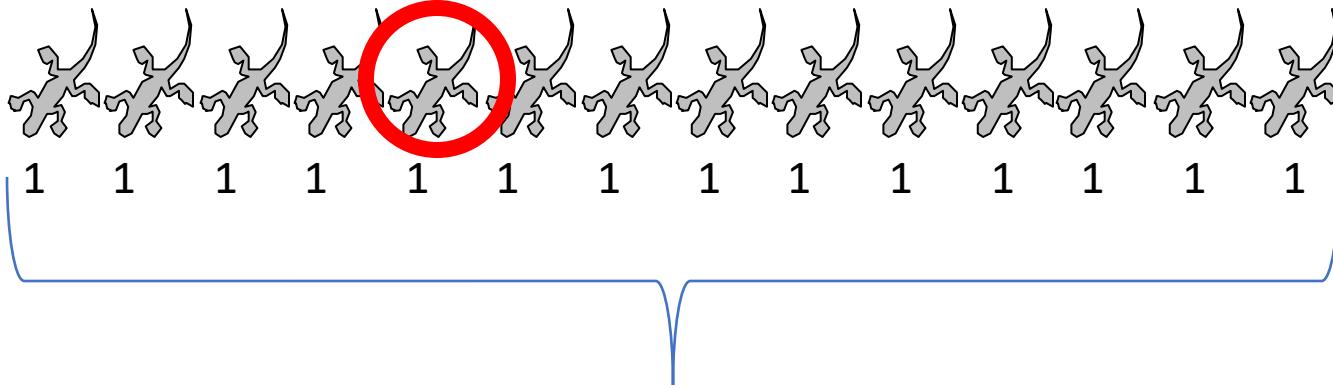


J=14  
N=14



Observation

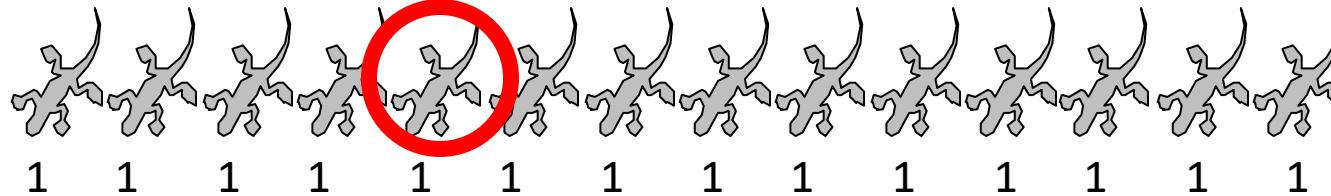
J=14  
N=14



Observation

Each has  $1/14$  chance

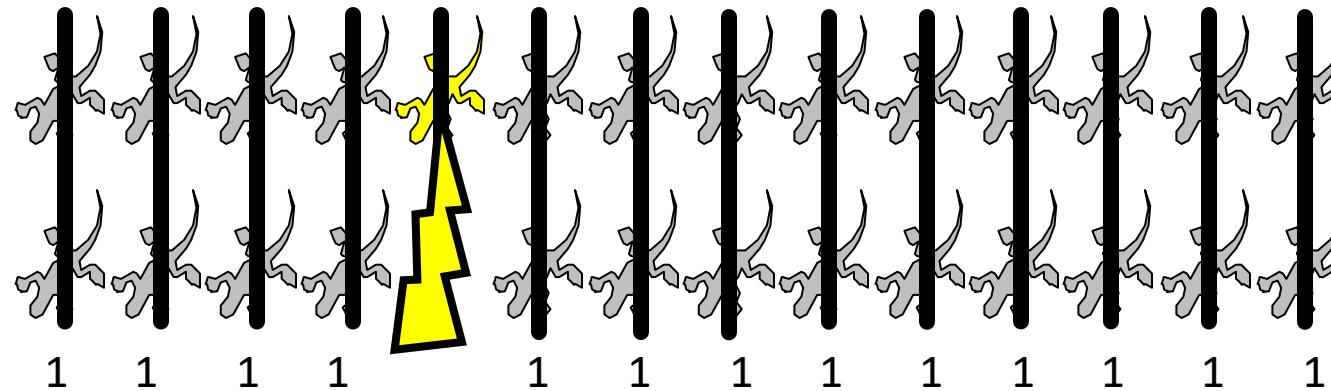
J=14  
N=14



Observation

Speciation

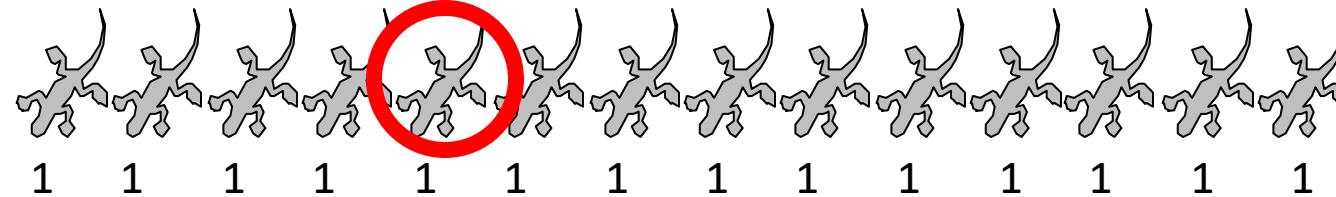
$\nu$



Observation

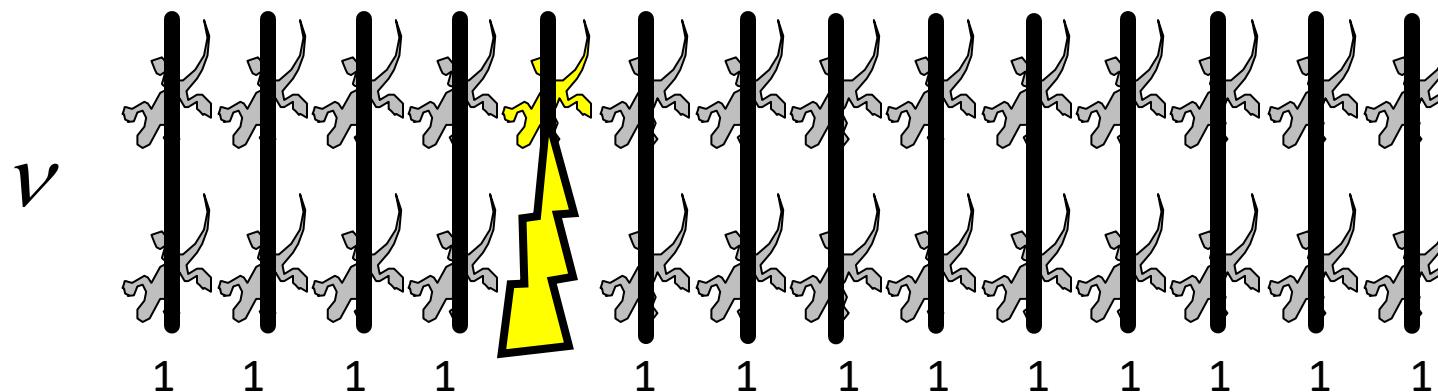
[ 1 ]

J=14  
N=14



Observation

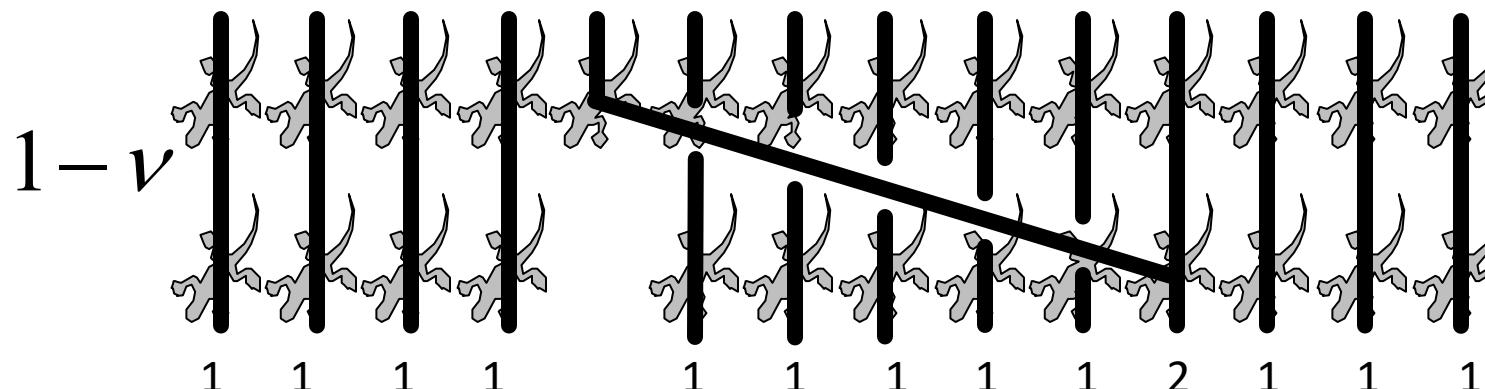
Speciation



Observation

[ 1 ]

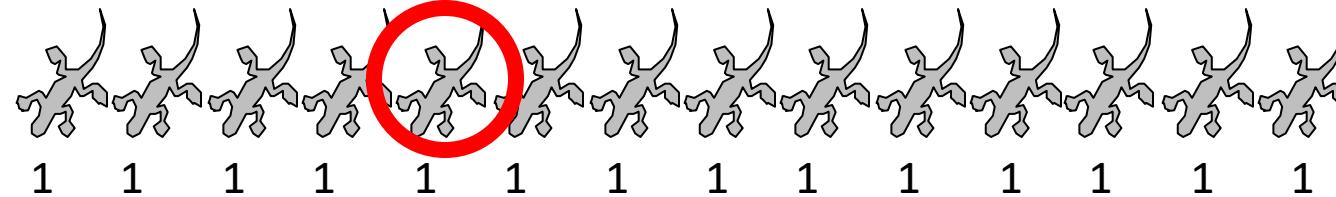
Coalescence



Observation

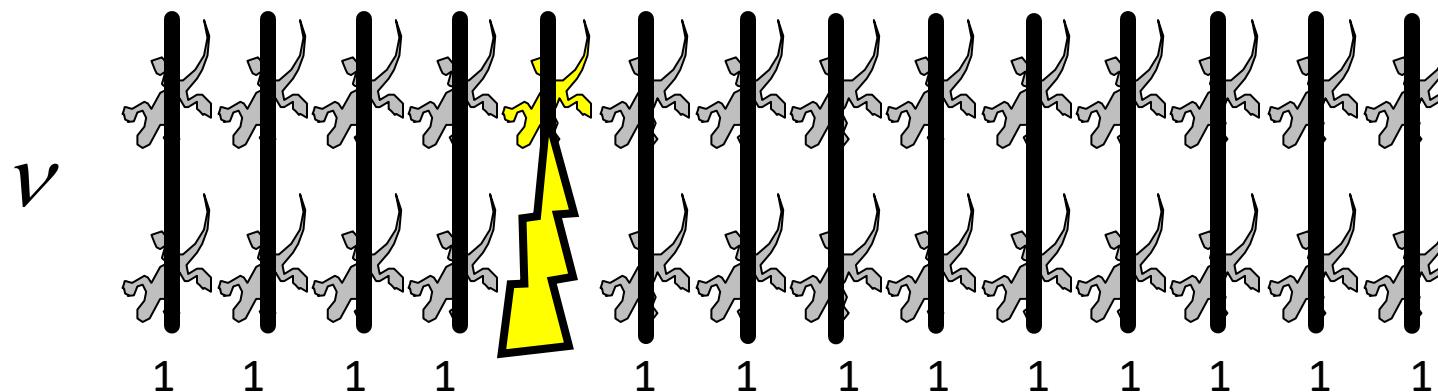
Each has 1/13 chance

J=14  
N=14



Observation

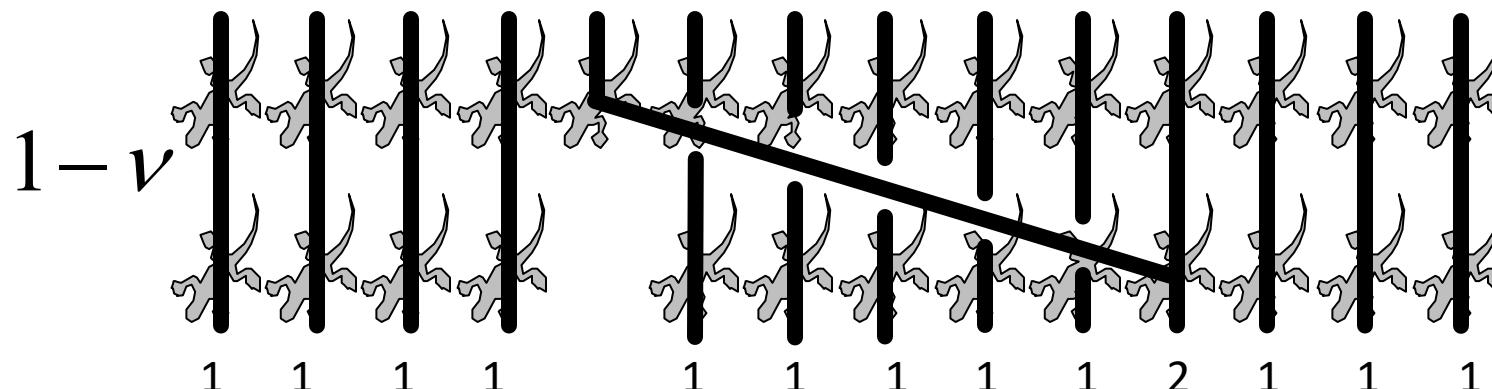
Speciation



Observation

[ 1 ]

Coalescence



Observation

J=14  
N=13

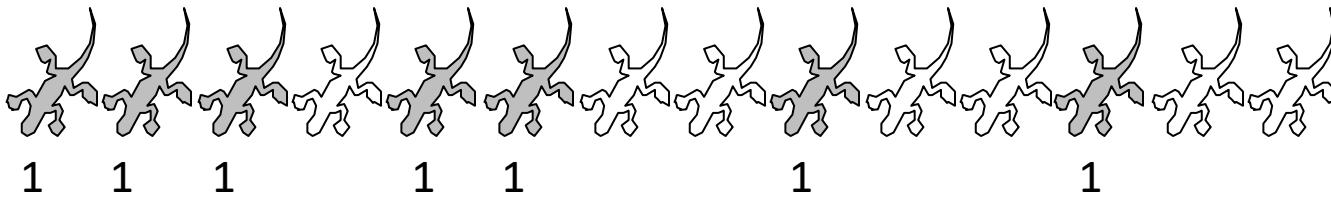
Each has 1/13 chance

J=14  
N=7



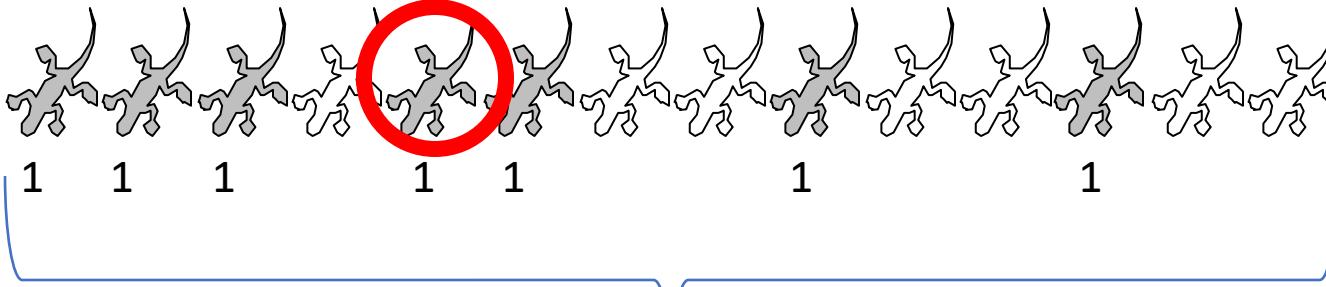
← Observation

$J=14$   
 $N=7$



← Observation

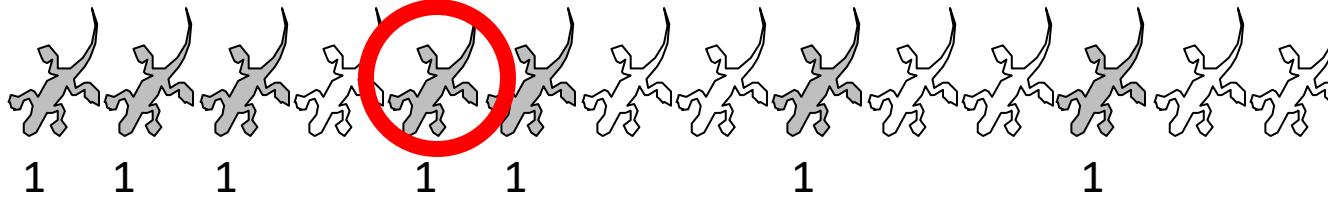
J=14  
N=7



Observation

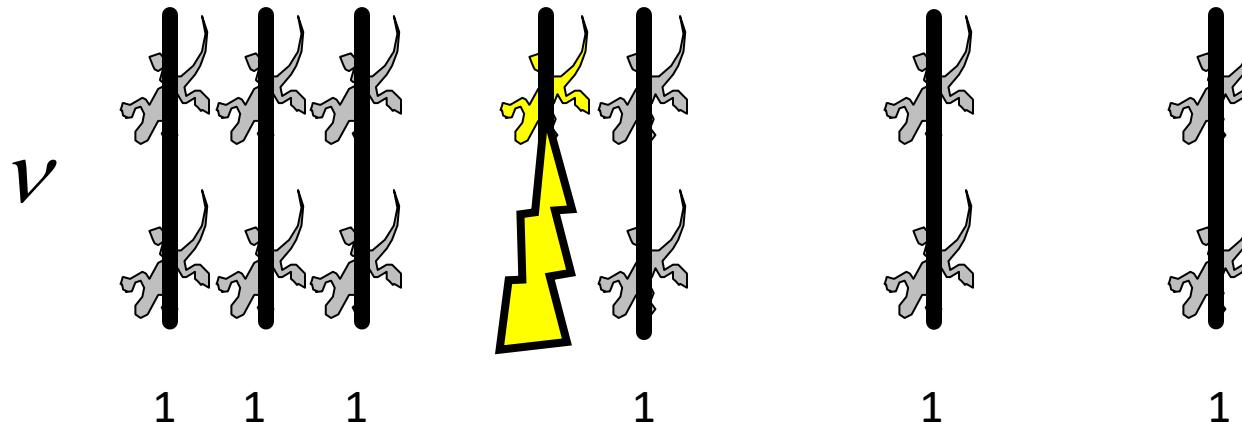
Each has 1/7 chance

J=14  
N=7



Observation

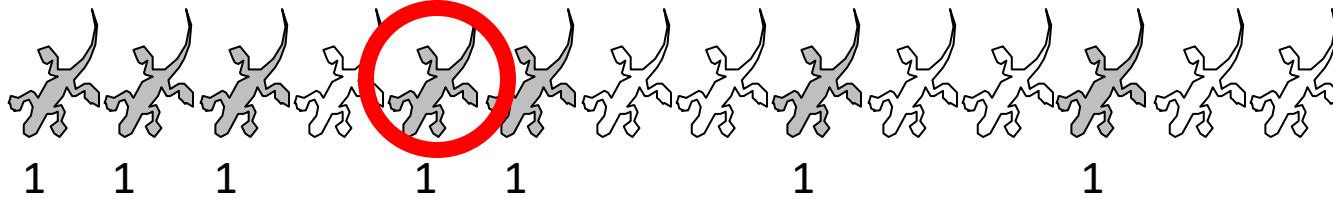
Speciation



Observation

[ 1 ]

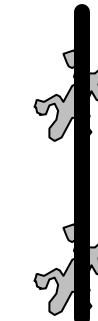
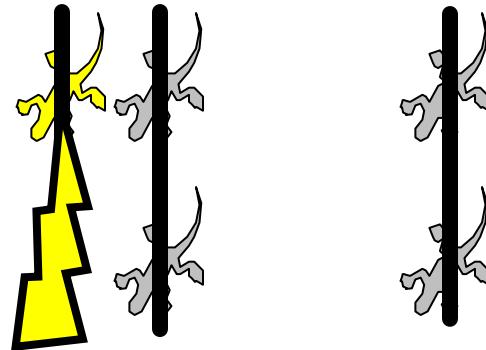
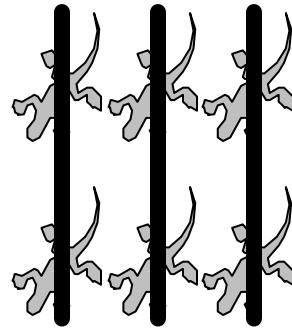
$J=14$   
 $N=7$



Observation

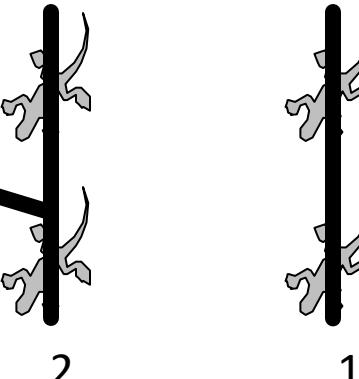
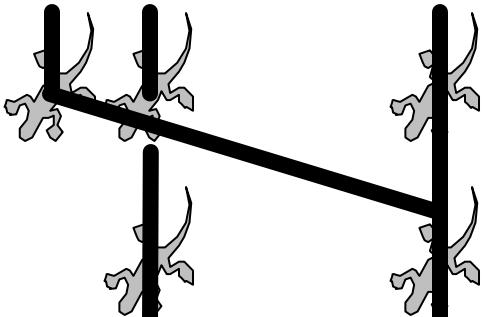
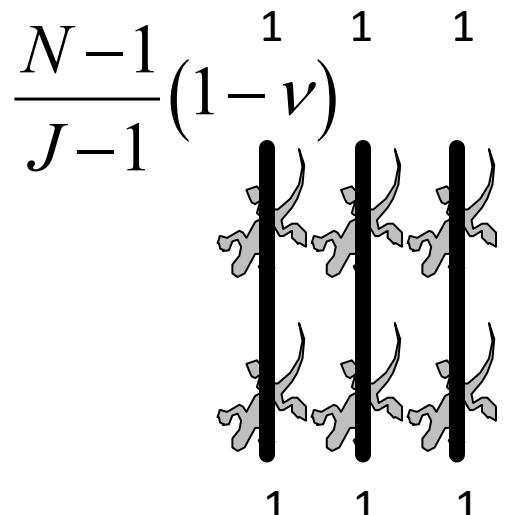
Speciation

$\nu$



Observation

[ 1 ]



Observation

Each has 1/6 chance

# Advantages of coalescence

- Always at equilibrium
- Much faster
- Sampling based

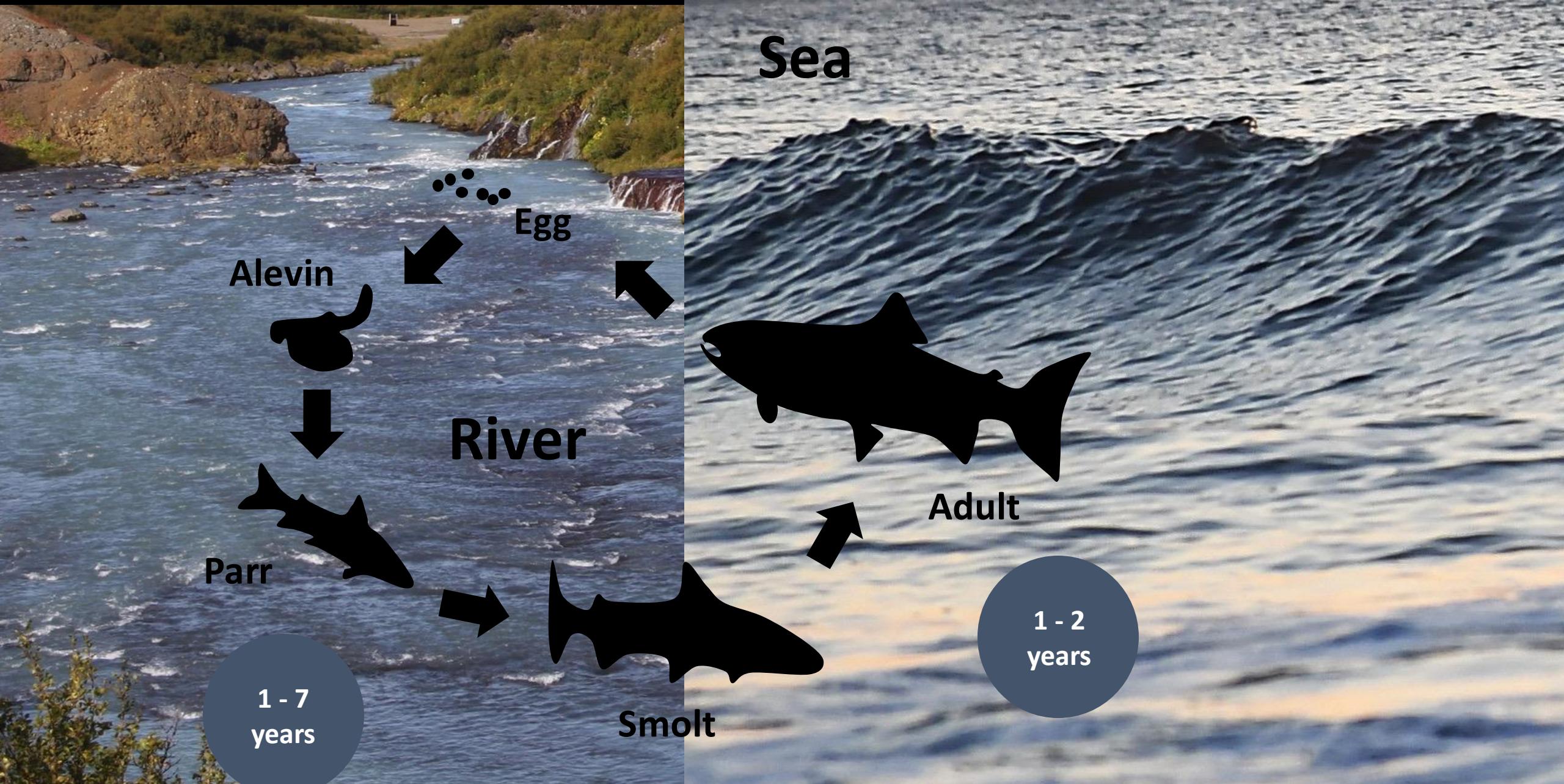
# Disadvantages of coalescence

- Not ideal for time series
- Complex to program
- Fewer ways in which model can be changed

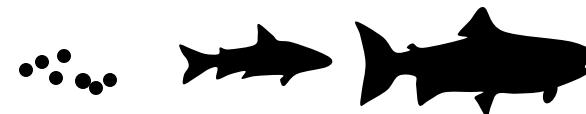
# Contents

- Coalescence methods in neutral theory
- Eigen Vectors and Eigen Values intuition
- Extinction debt and habitat fragmentation example

# Atlantic Salmon life cycle



# Atlantic Salmon toy matrix population model



$$\begin{pmatrix} 0.2 & 0 & 10 \\ 0.2 & 0.3 & 0 \\ 0 & 0.1 & 0.4 \end{pmatrix} \begin{pmatrix} 0 \\ 0 \\ 100 \end{pmatrix}$$

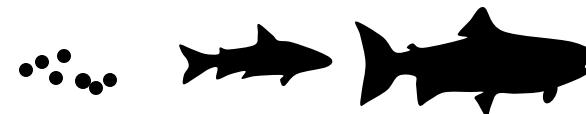
After 1  
time step

$$\begin{pmatrix} ? \\ ? \\ ? \end{pmatrix}$$

After 2  
time steps

$$\begin{pmatrix} ? \\ ? \\ ? \end{pmatrix}$$

# Atlantic Salmon toy matrix population model



$$\begin{pmatrix} 0.2 & 0 & 10 \\ 0.2 & 0.3 & 0 \\ 0 & 0.1 & 0.4 \end{pmatrix} \begin{pmatrix} 0 \\ 0 \\ 100 \end{pmatrix}$$

**A**                           **V**

After 1  
time step

$$\begin{pmatrix} 1,000 \\ 0 \\ 40 \end{pmatrix}$$

**Av**

After 2  
time steps

$$\begin{pmatrix} 600 \\ 200 \\ 16 \end{pmatrix}$$

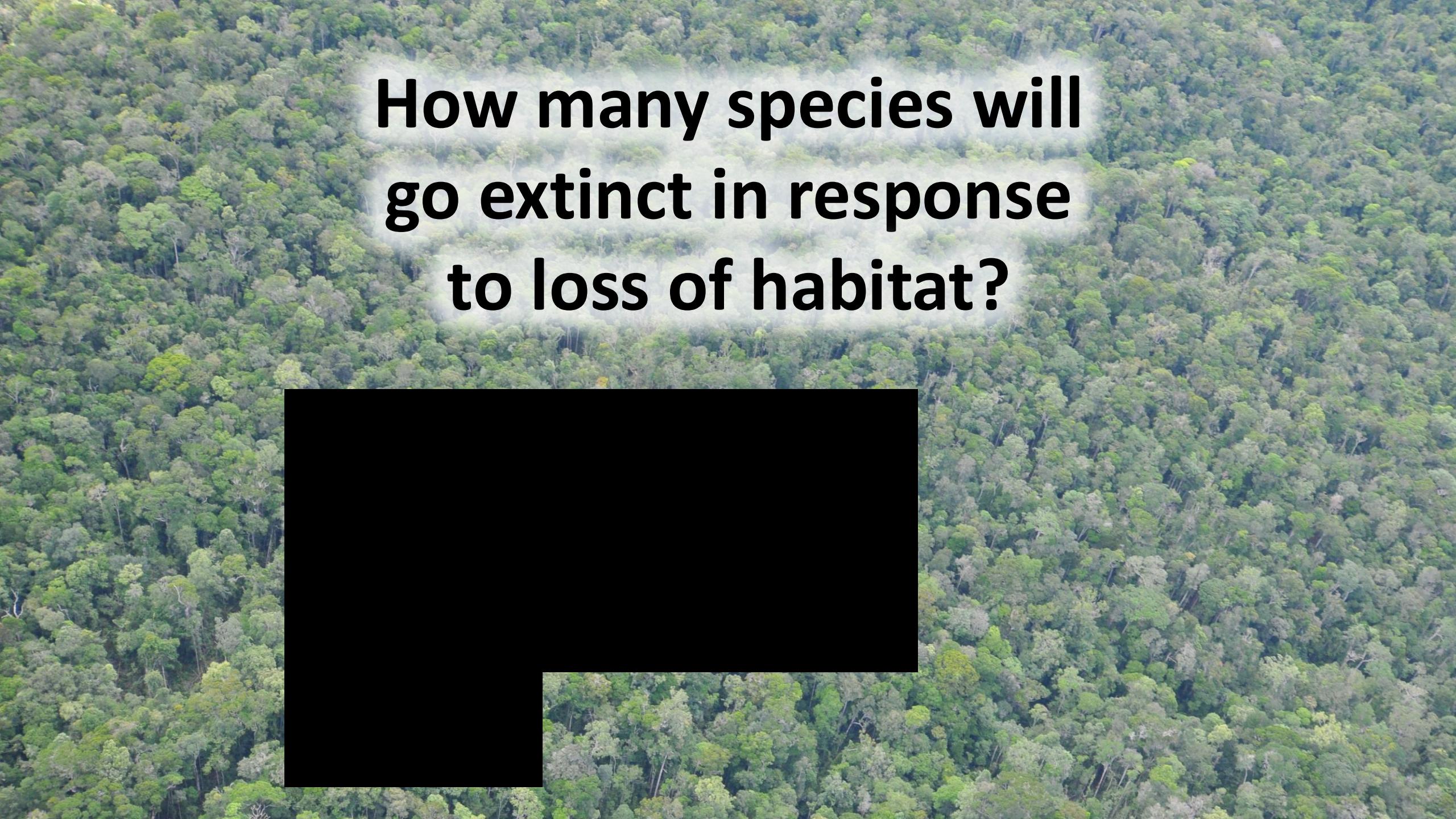
**$A^2V$**

# What is an eigen vector and value

$$A\boldsymbol{v} = \lambda\boldsymbol{v}$$

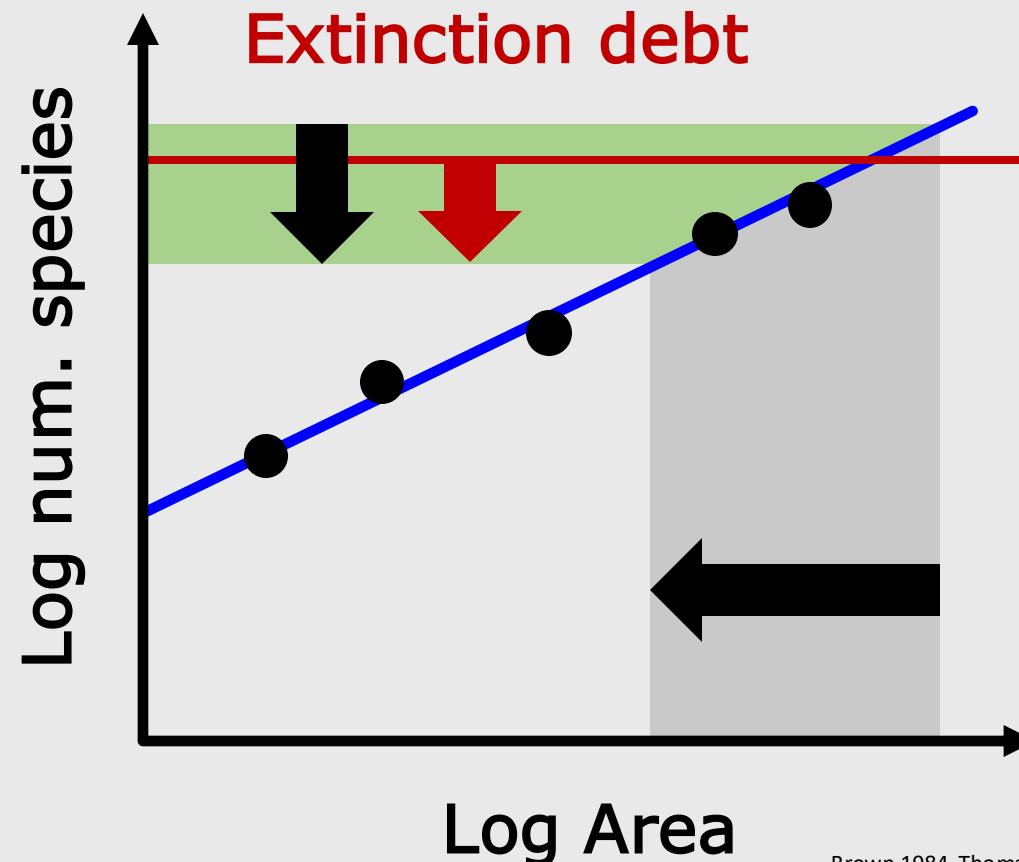
Matrix                      Eigenvalue  
↓                            ↓  
                                  
Eigenvector                  Eigenvector

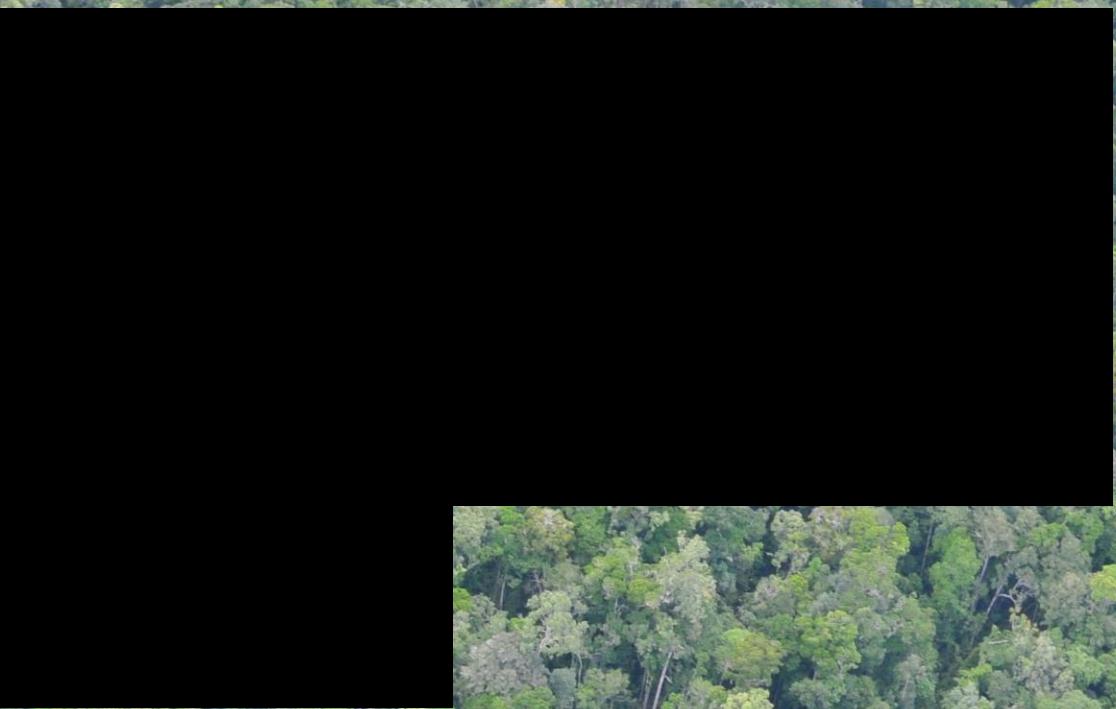
```
graph TD; Matrix[Matrix] --> Av[A*v]; Lambda[Eigenvalue] --> Av; Av --> Eigenvector[Eigenvector]
```



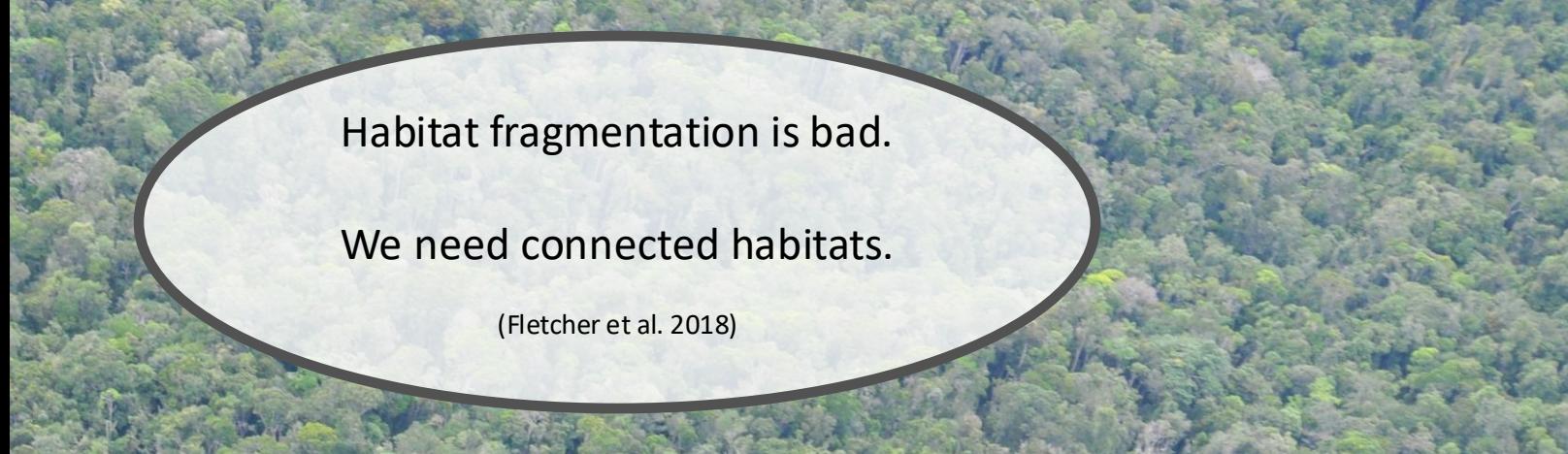
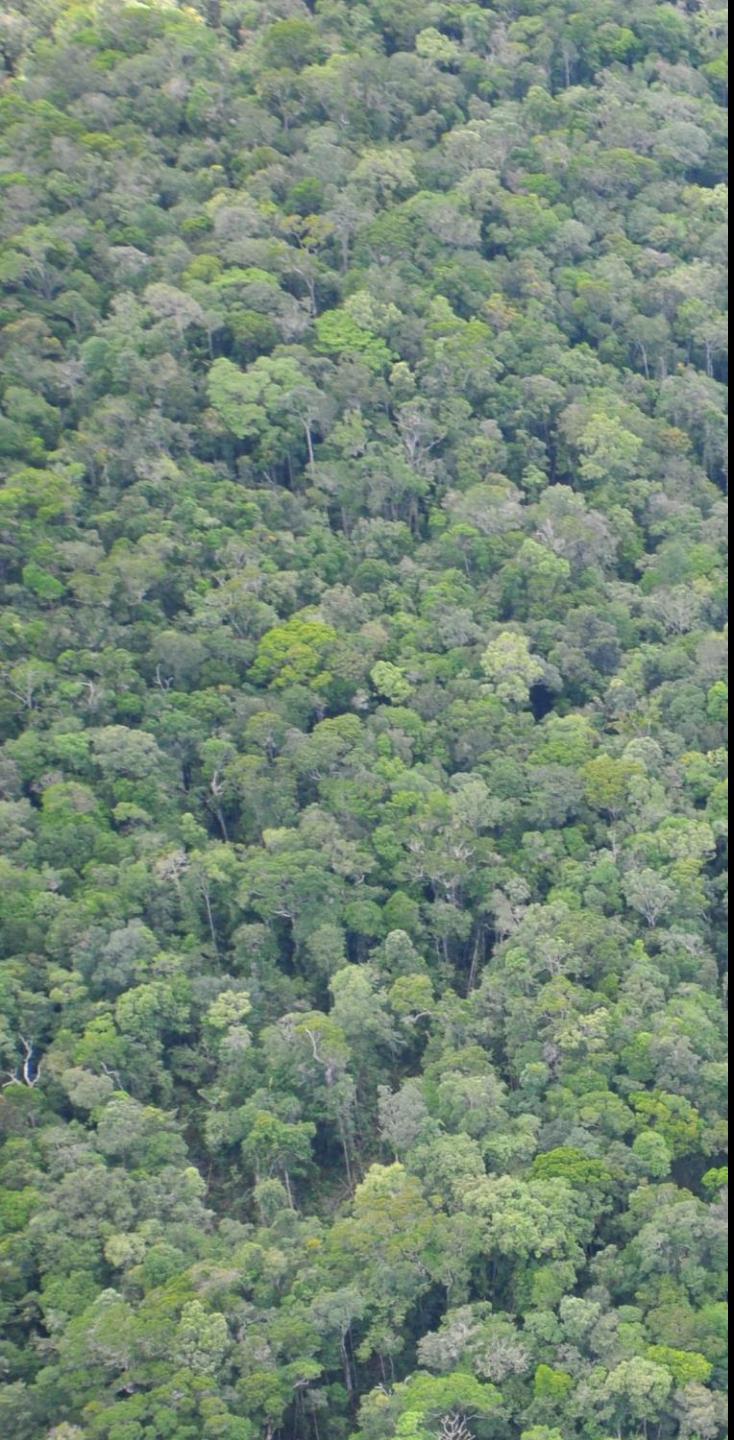
**How many species will  
go extinct in response  
to loss of habitat?**

# Species area relationships and species loss







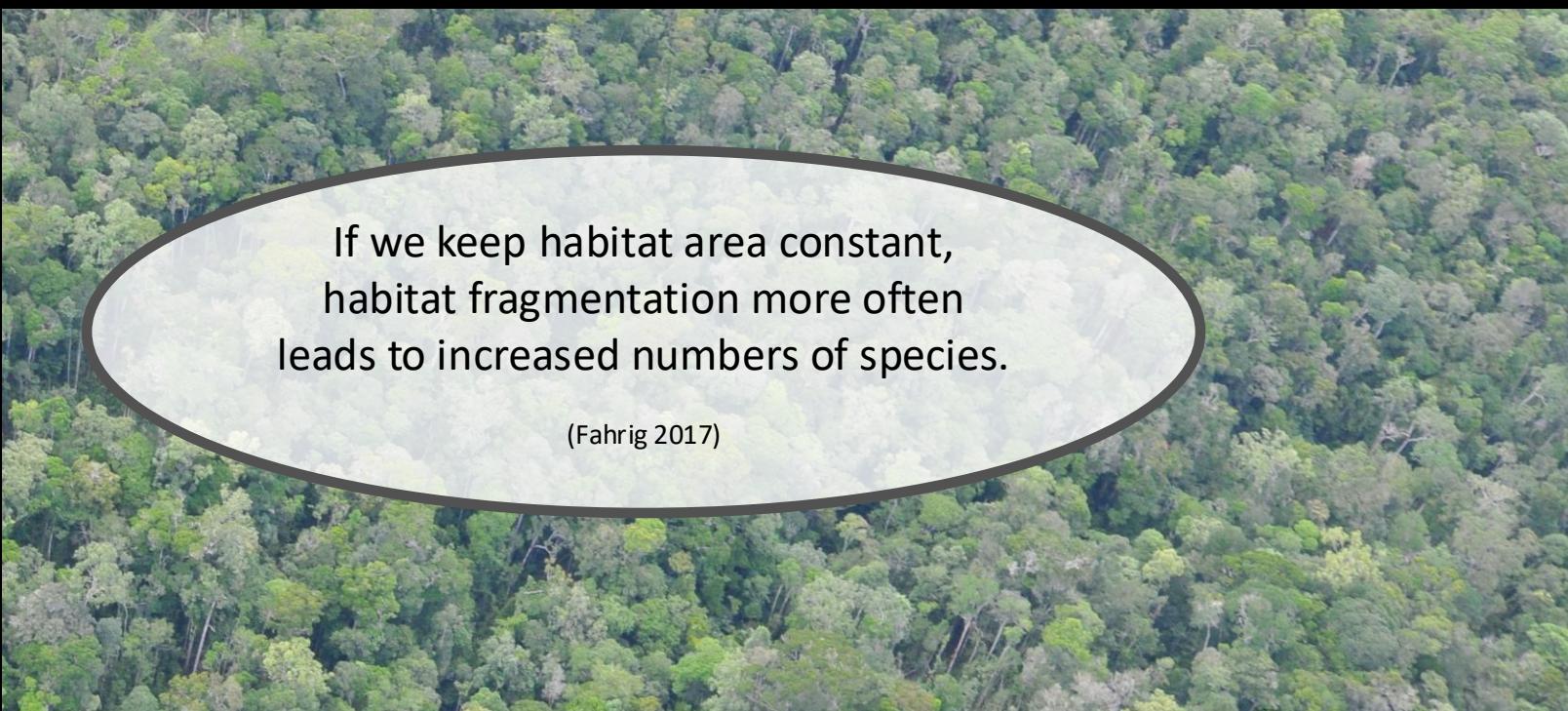


Habitat fragmentation is bad.

We need connected habitats.

(Fletcher et al. 2018)

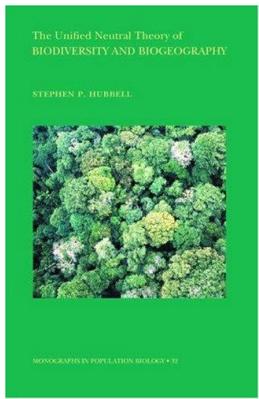
Fragmentation:  
“breaking or being broken into fragments”  
(Oxford Languages)



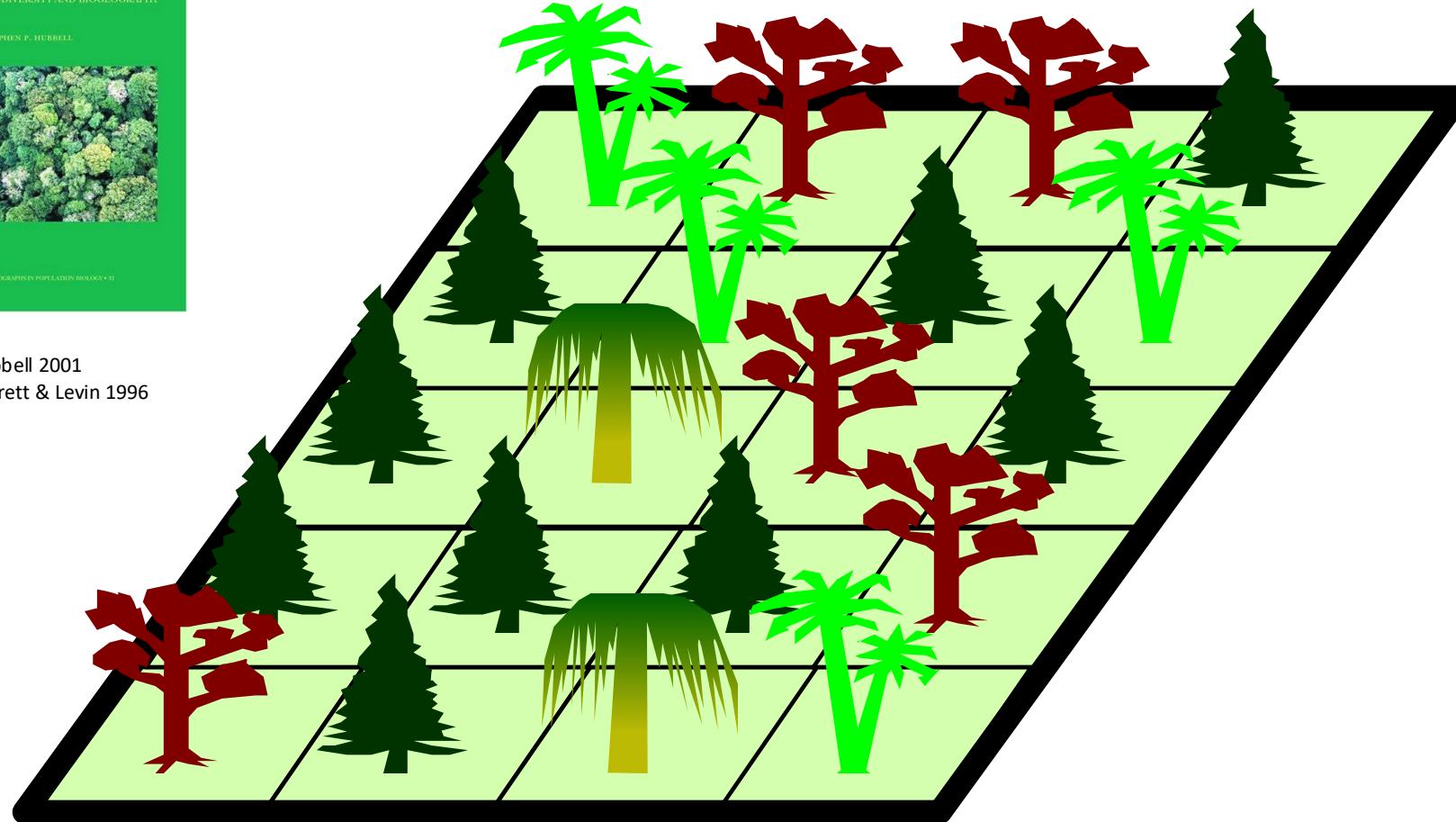
If we keep habitat area constant,  
habitat fragmentation more often  
leads to increased numbers of species.

(Fahrig 2017)

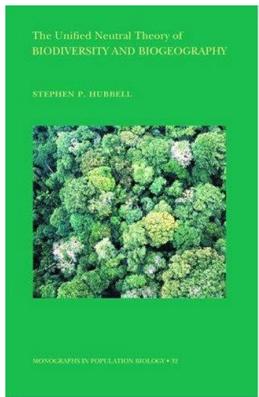
# Neutral models in ecology



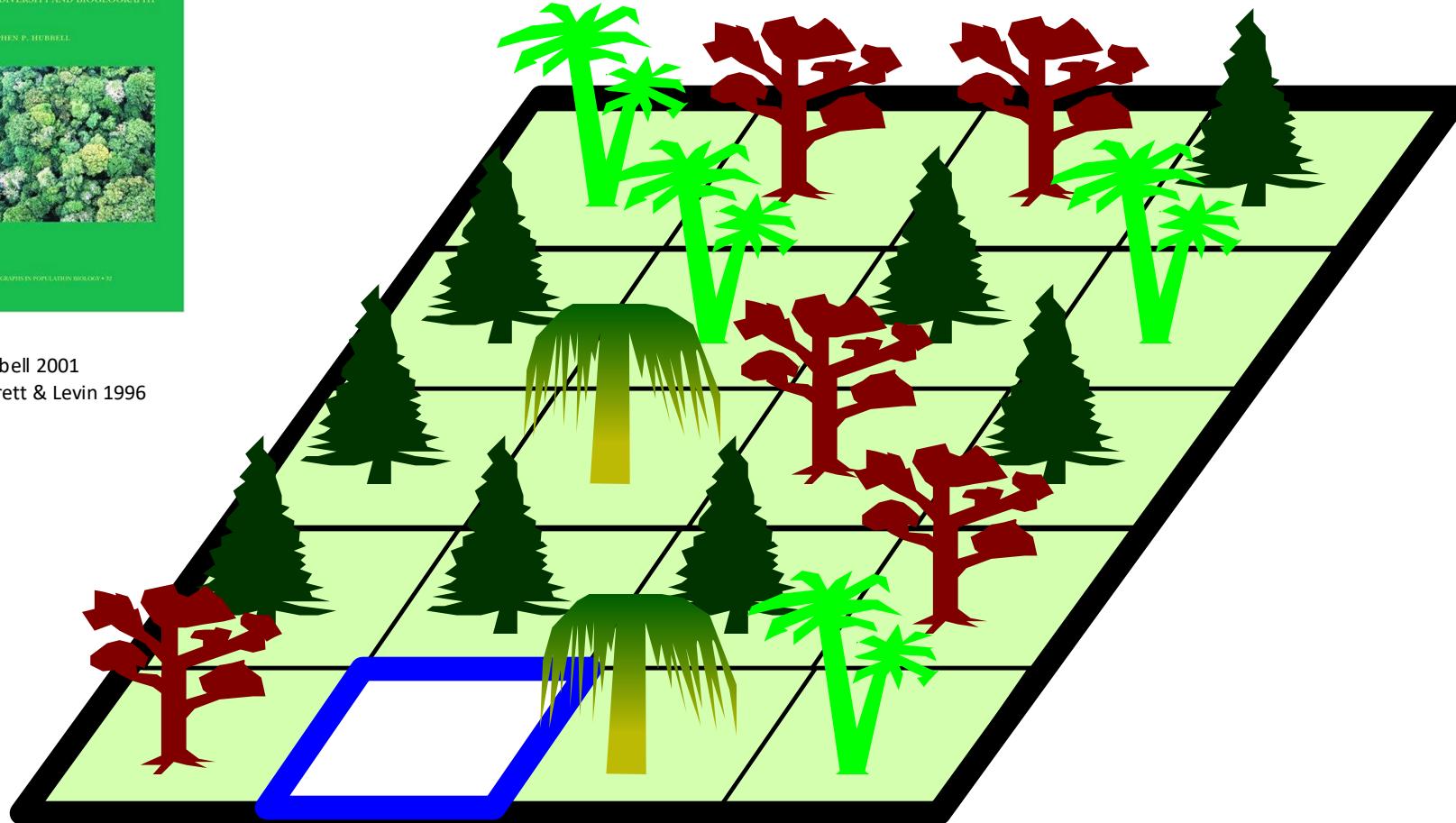
Hubbell 2001  
Durrett & Levin 1996



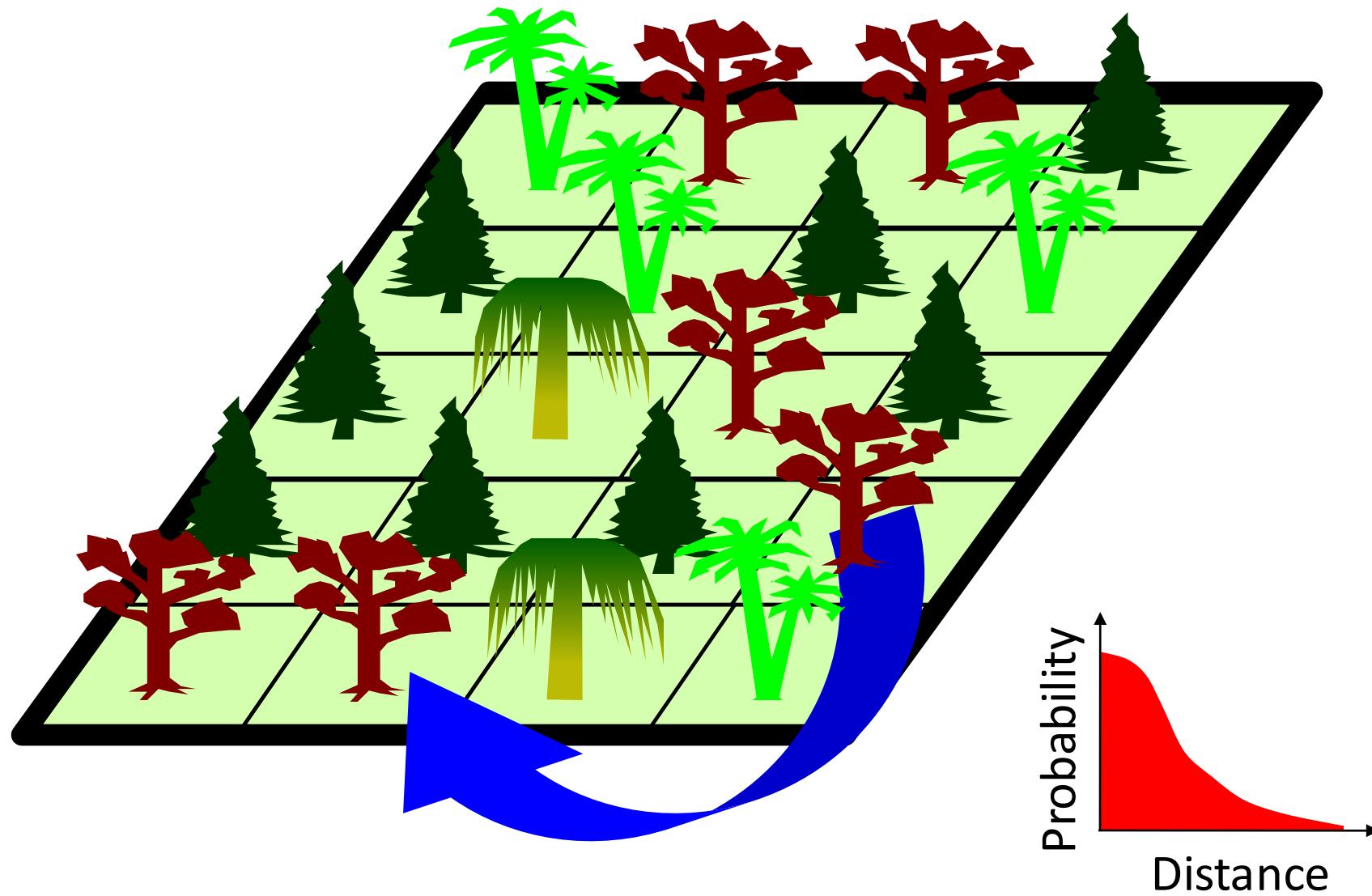
# Neutral models in ecology



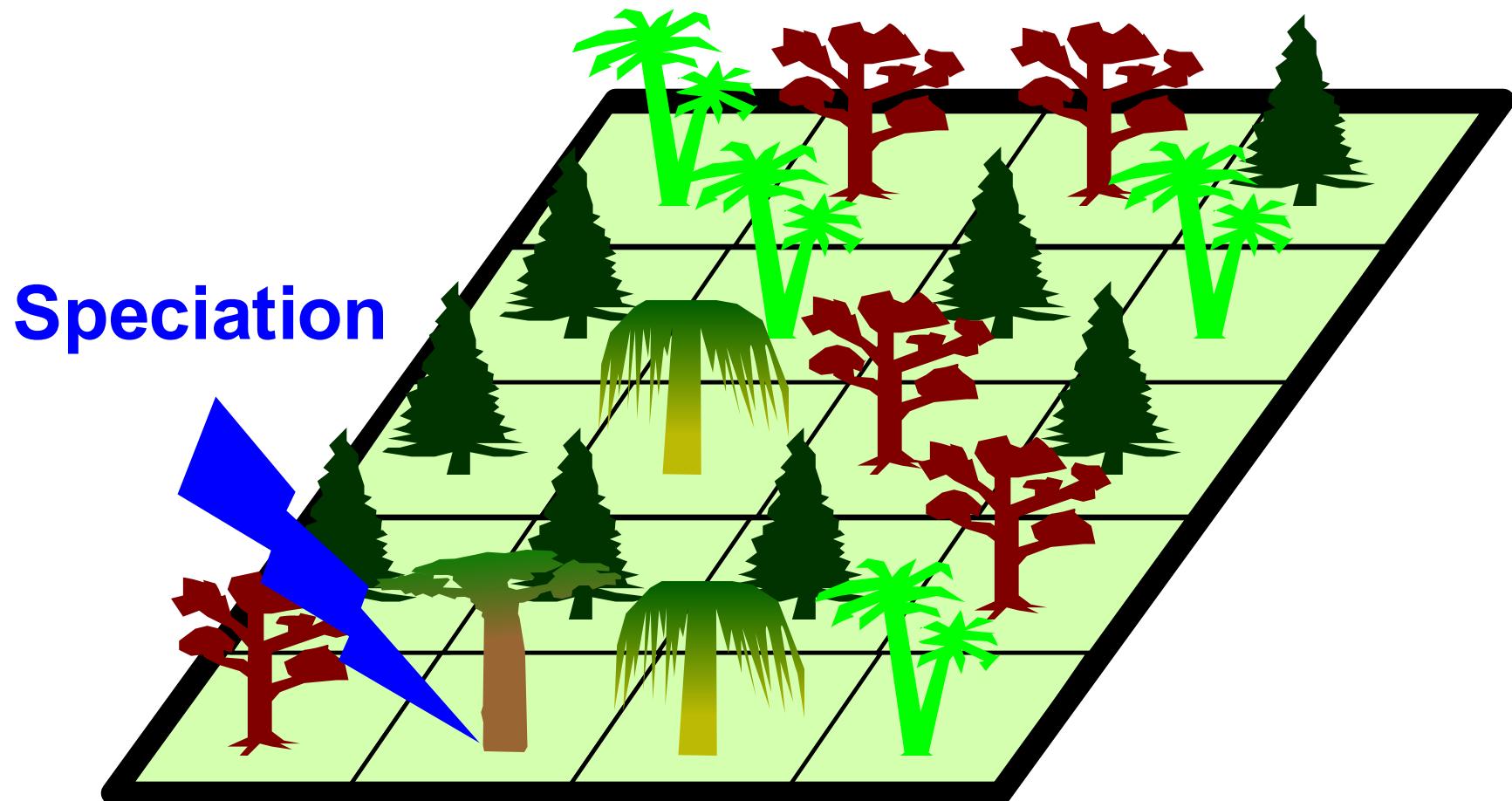
Hubbell 2001  
Durrett & Levin 1996



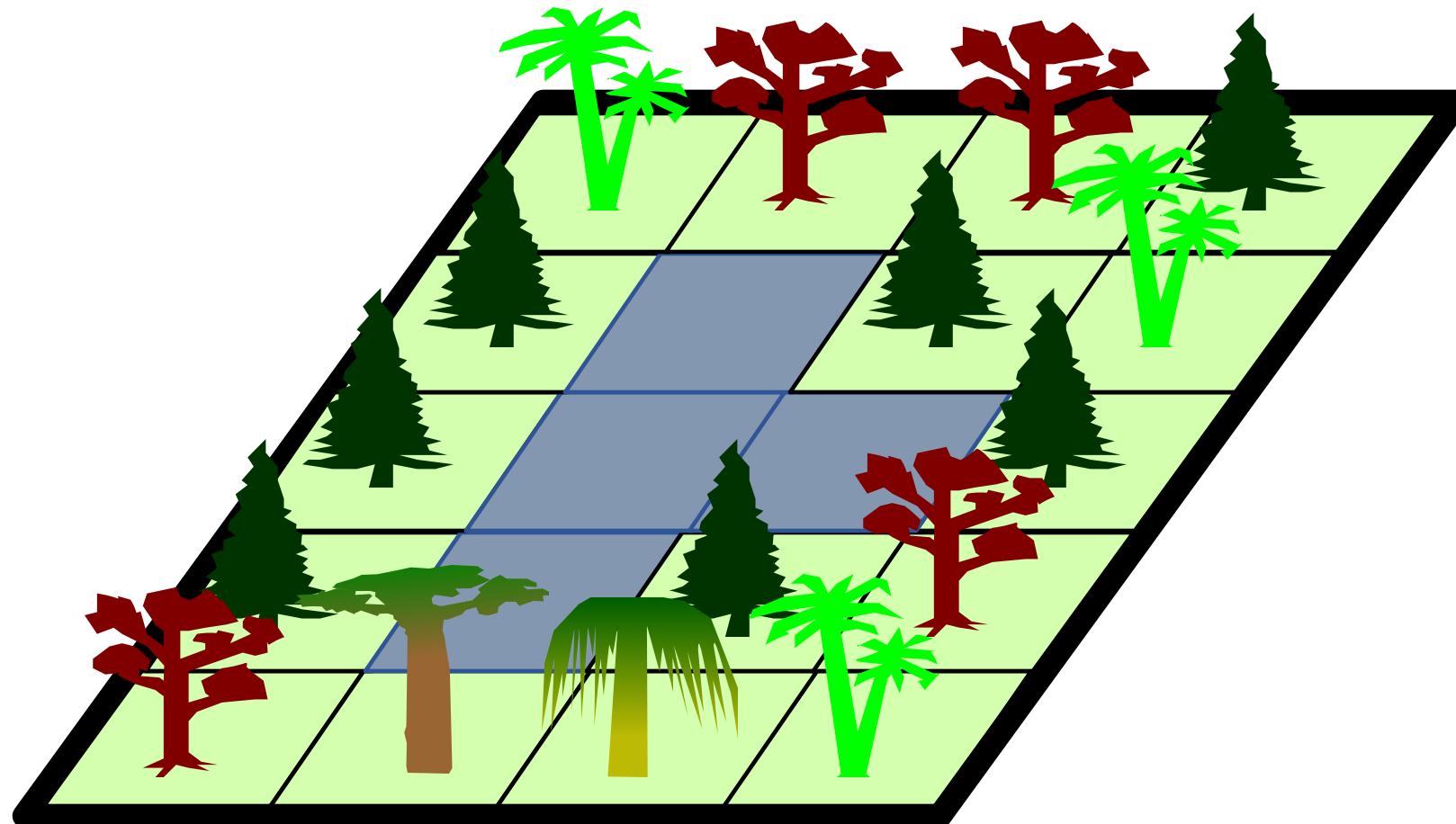
# Neutral models in ecology

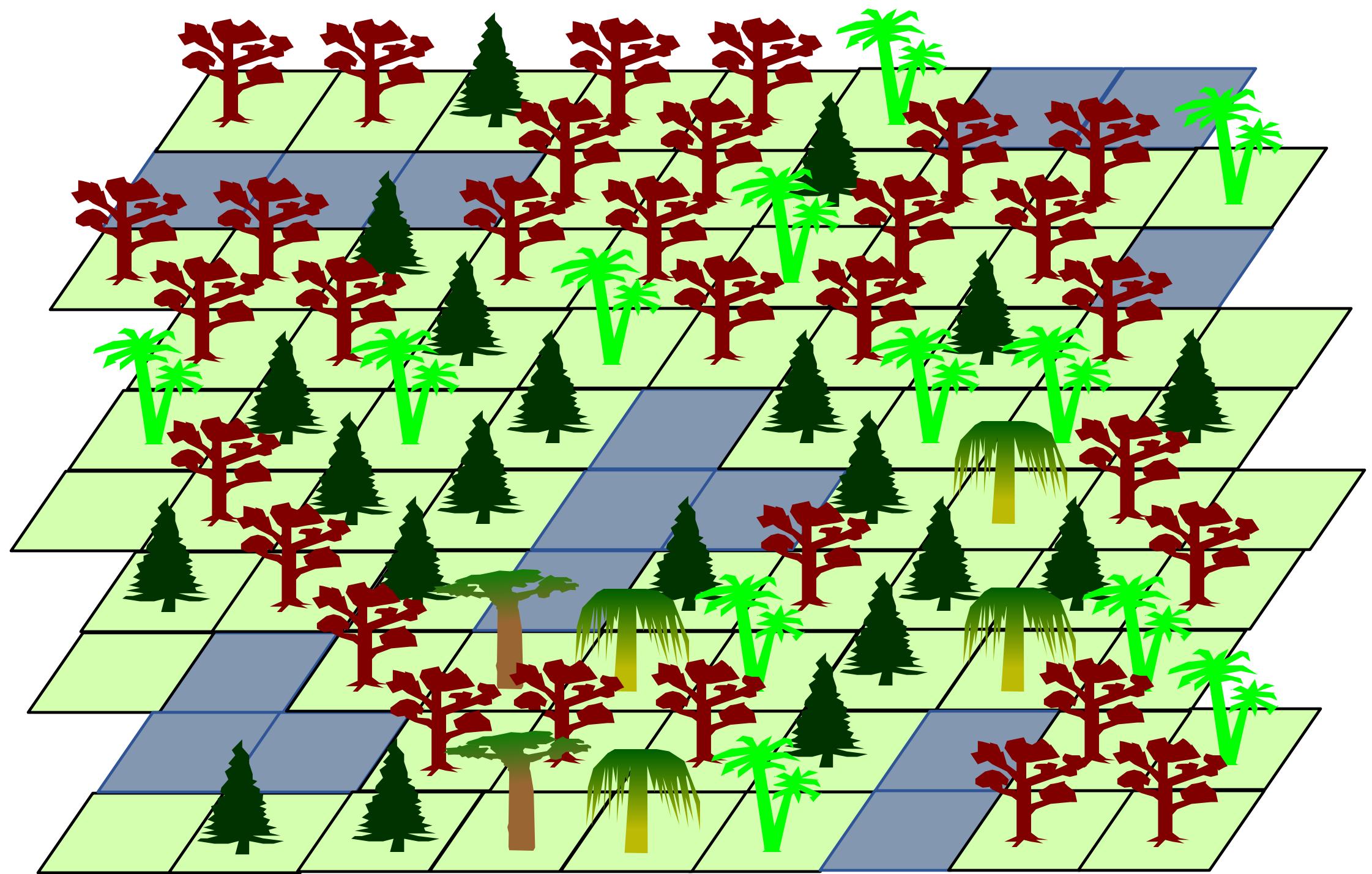


# Neutral models in ecology



# Neutral models in ecology





**Original num. species**



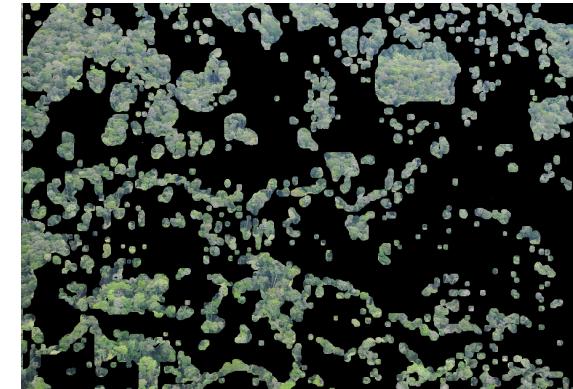
**Short-term best case num. species**



**Short-term worst case num. species**



**Long-term equilibrium num. species**



**Original num. species**



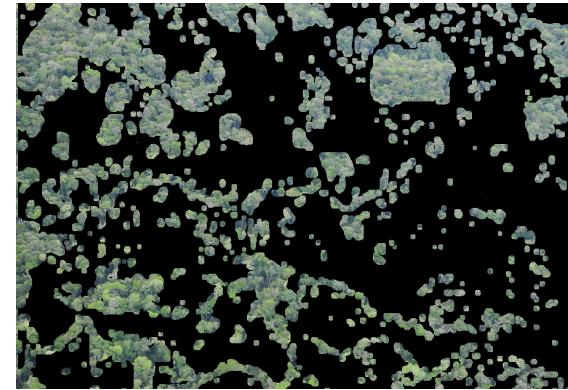
**Short-term best case num. species**



**Short-term worst case num. species**



**Long-term equilibrium num. species**



# Original area $A_{\max}$

Total number of individuals in original habitat

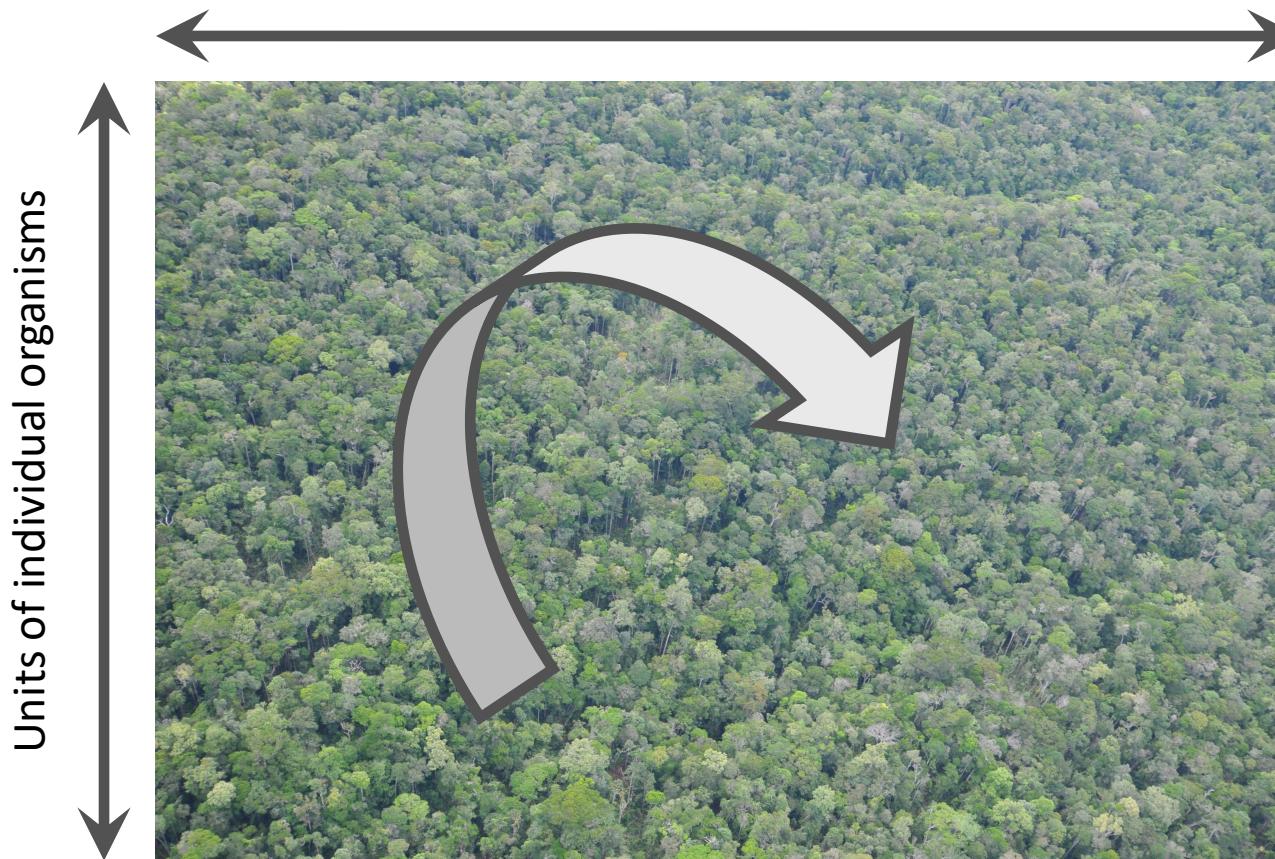


# Original area $A_{\max}$

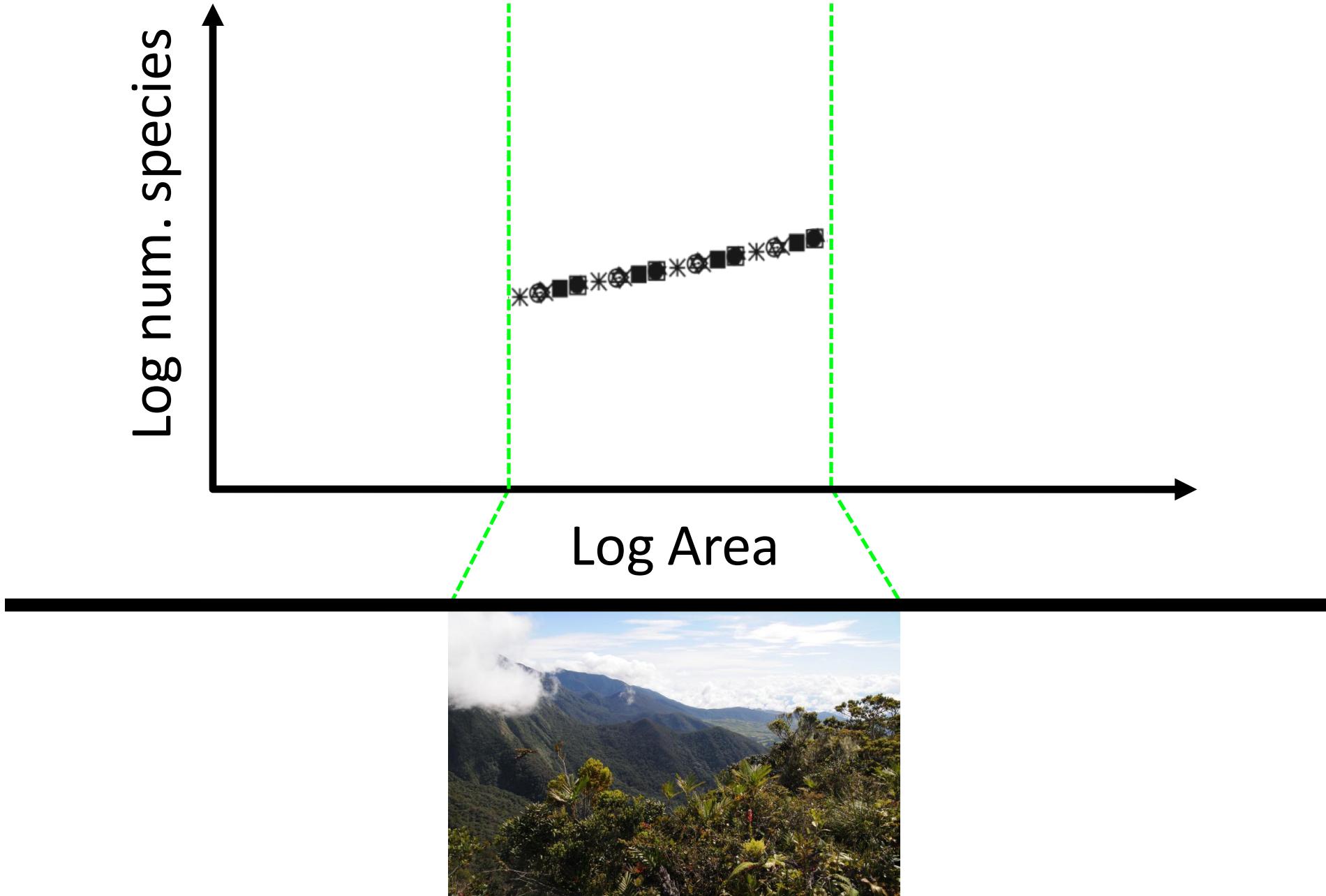
Total number of individuals in original habitat

## Intrinsic dispersal $\sigma$

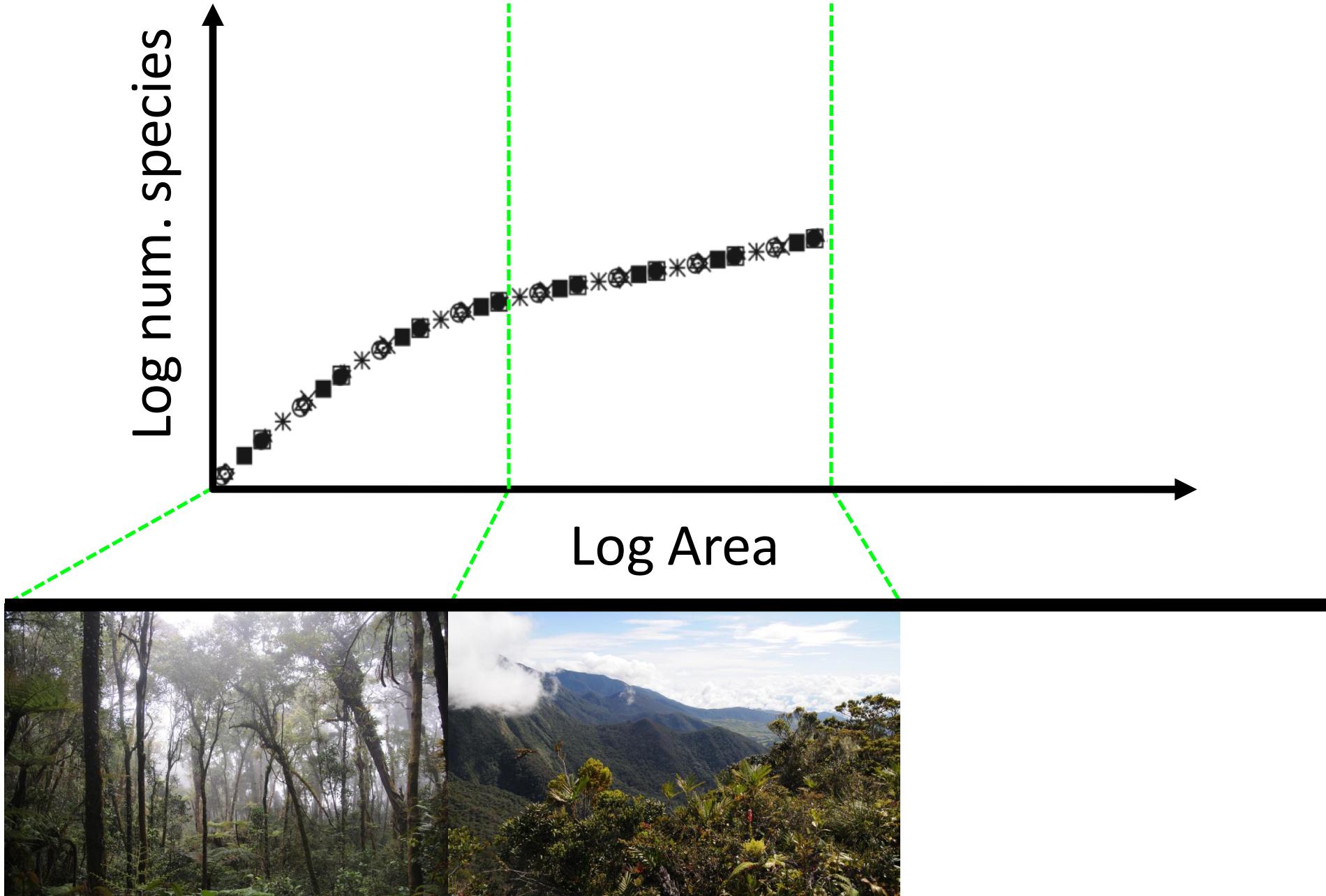
Based on the variance  $\sigma^2$  of the normal dispersal kernel



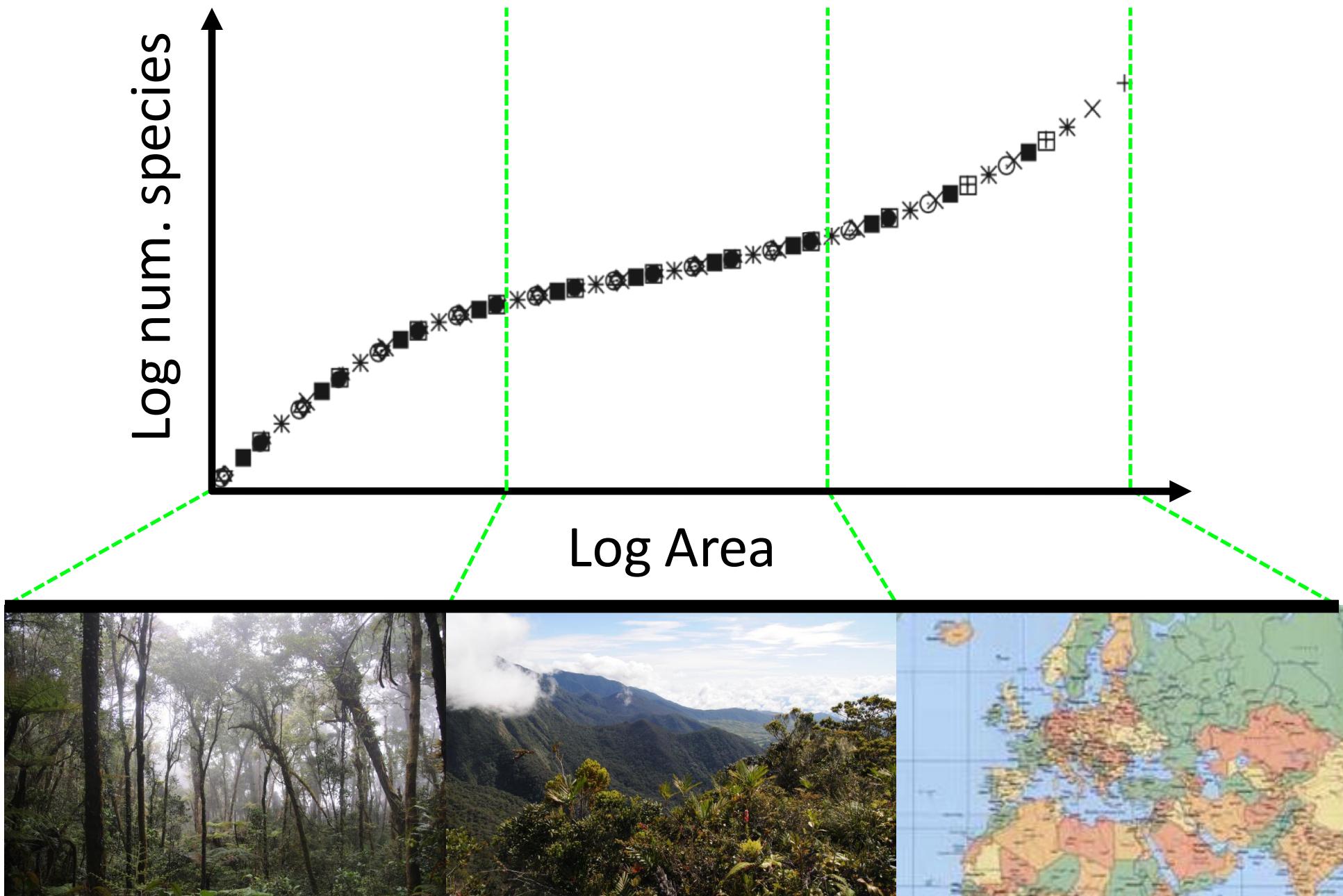
# Original richness - Species area relationship



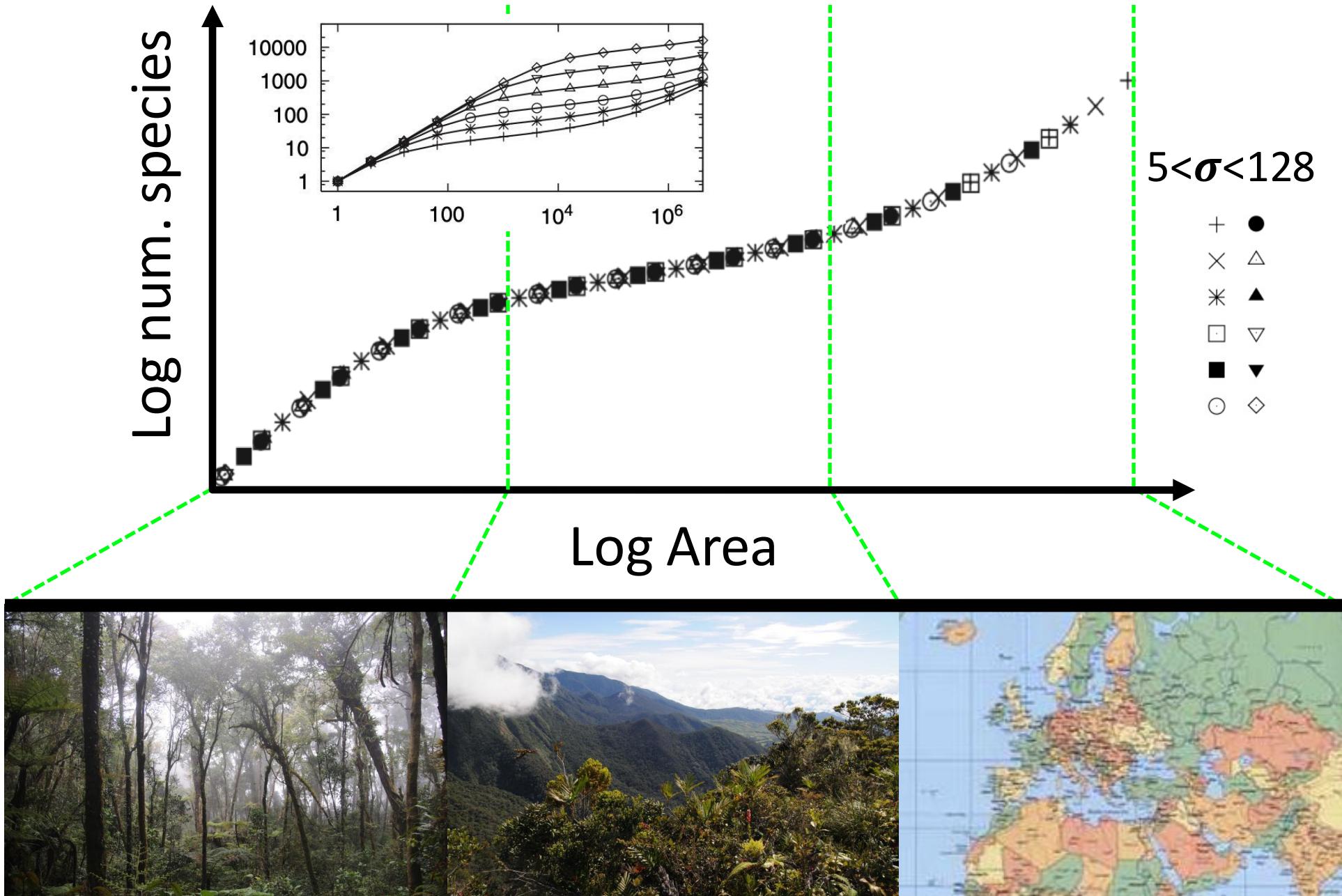
# Original richness - Species area relationship



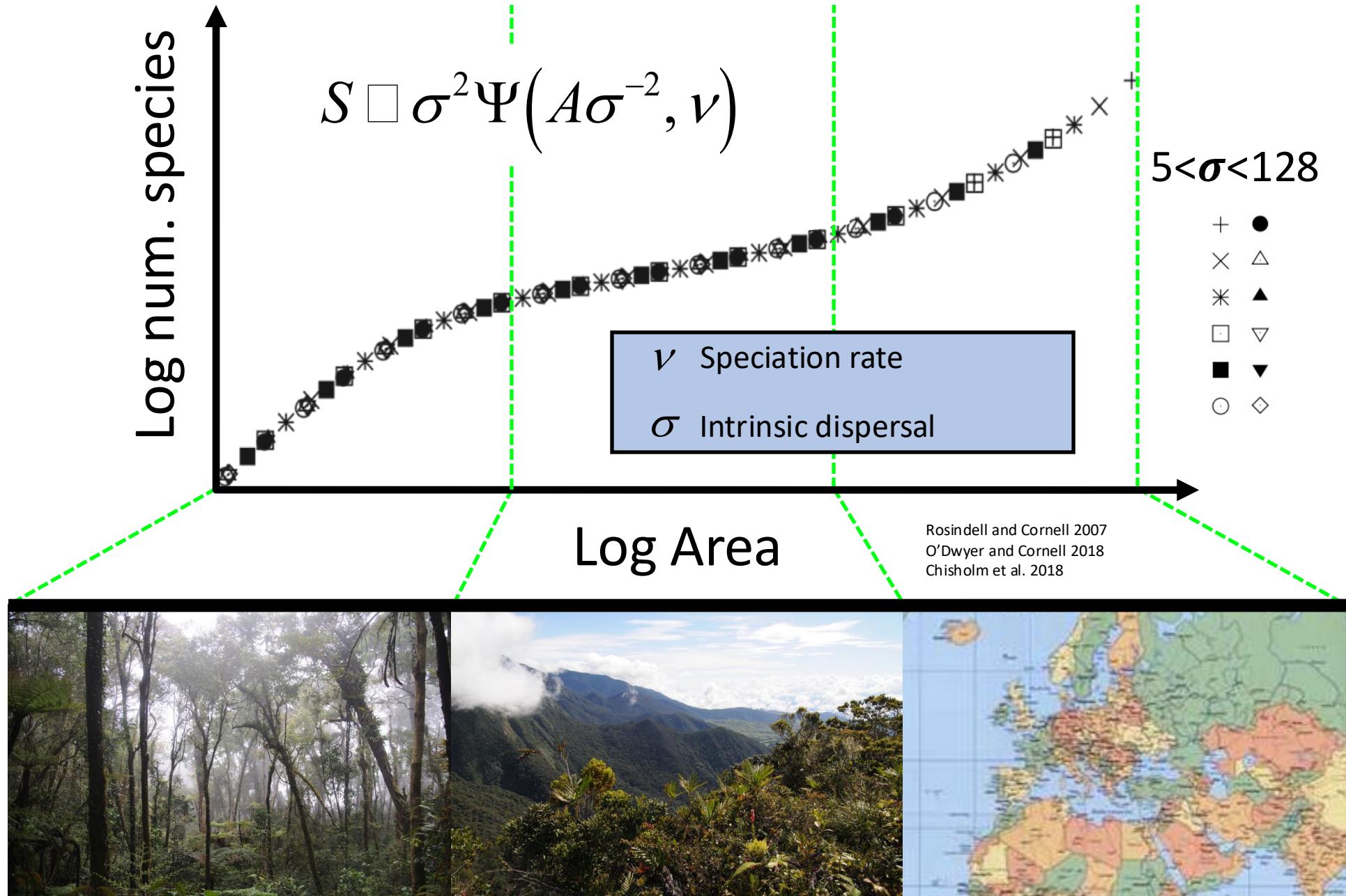
# Original richness - Species area relationship



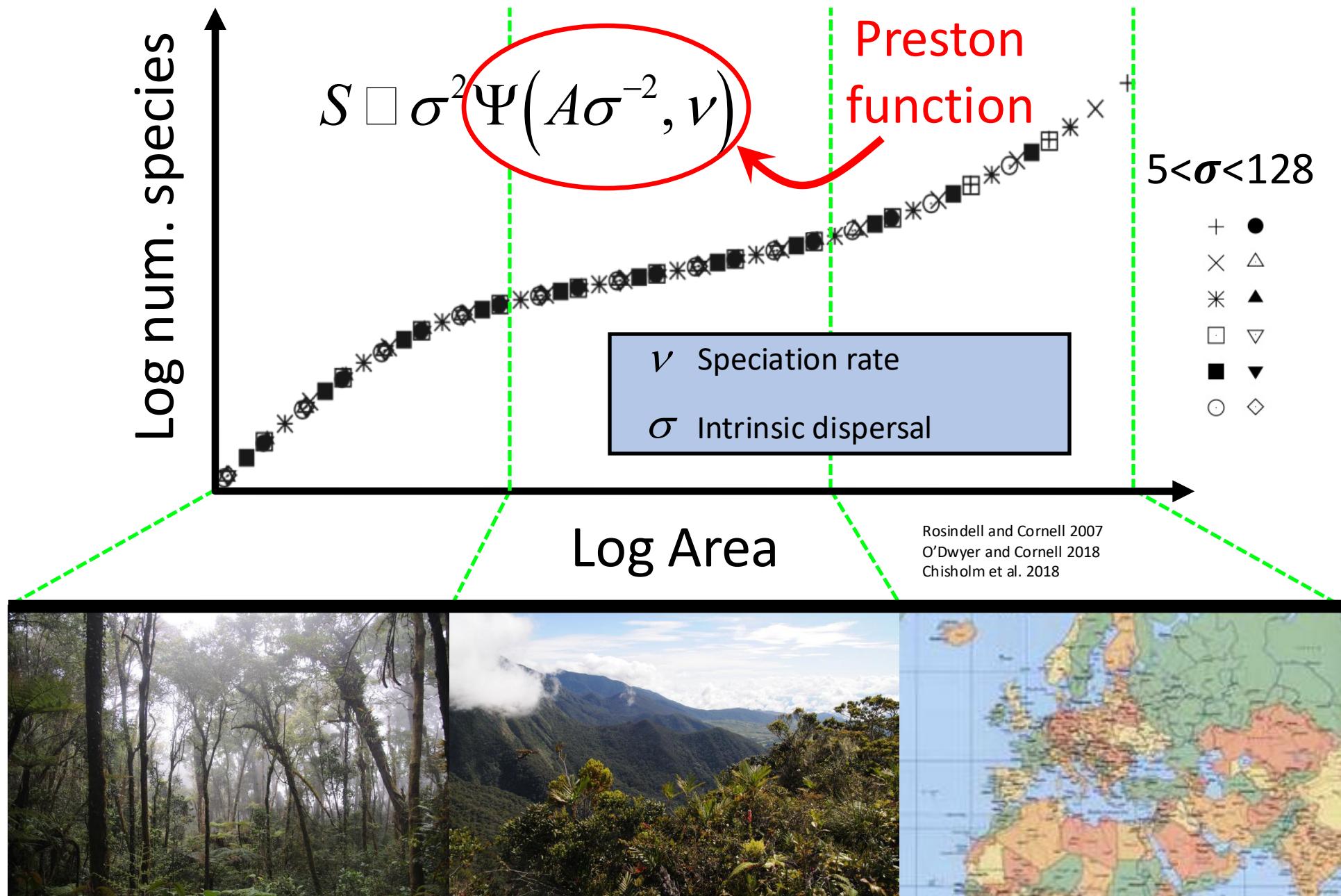
# Original richness - Species area relationship



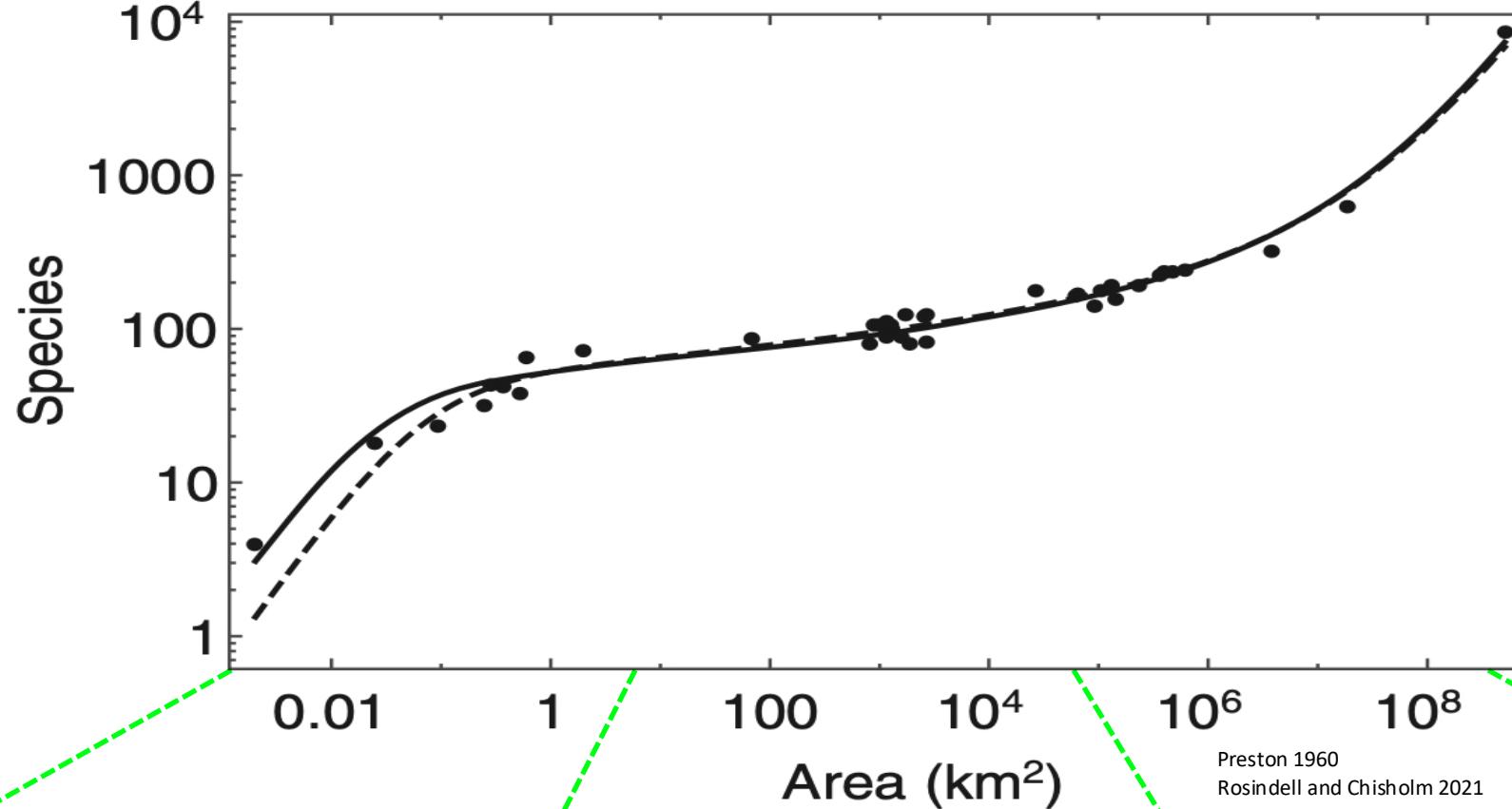
# Original richness - Species area relationship



# Original richness - Species area relationship



# Original richness - Species area relationship



**Original num. species**



**Short-term best case num. species**

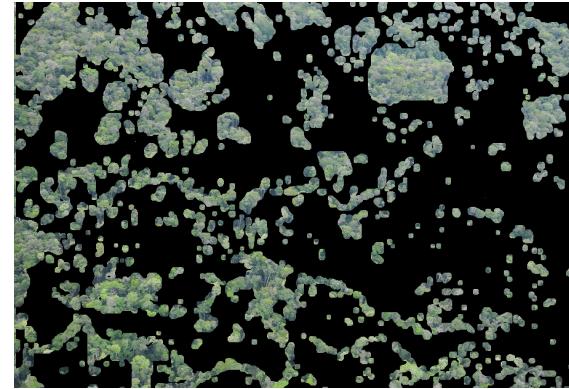


$$\sigma^2 \Psi\left(\frac{A_{\max}}{\sigma^2}, \nu\right)$$

**Short-term worst case num. species**



**Long-term equilibrium num. species**



**Original num. species**

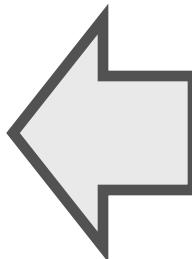


**Short-term best case num. species**

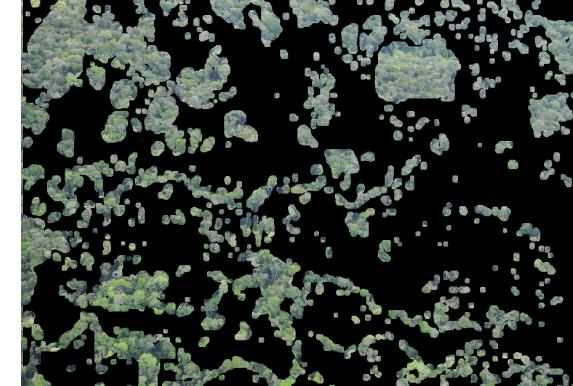


$$\sigma^2 \Psi\left(\frac{A_{\max}}{\sigma^2}, \nu\right)$$

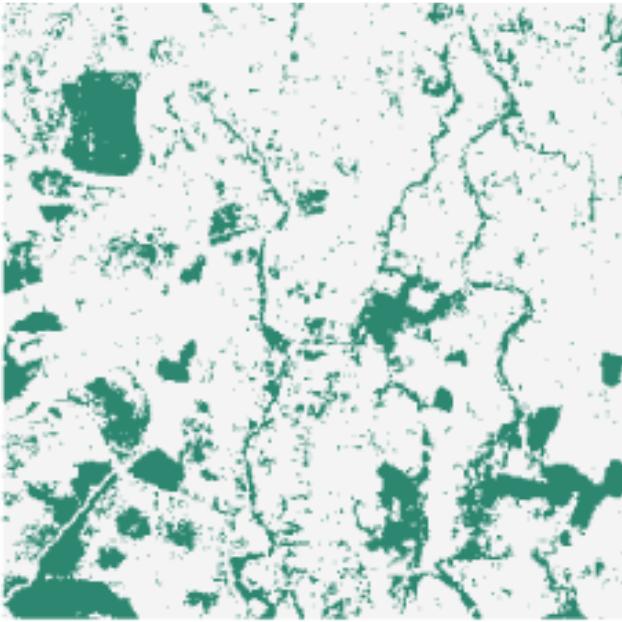
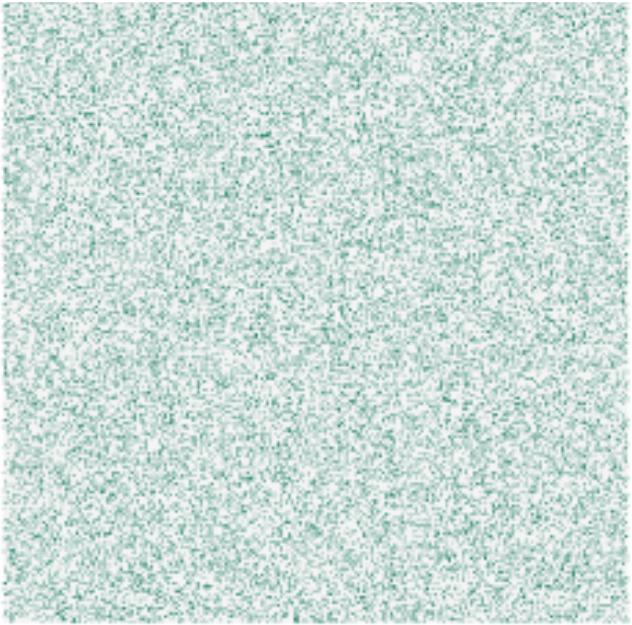
**Short-term worst case num. species**



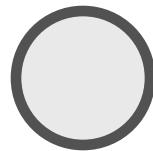
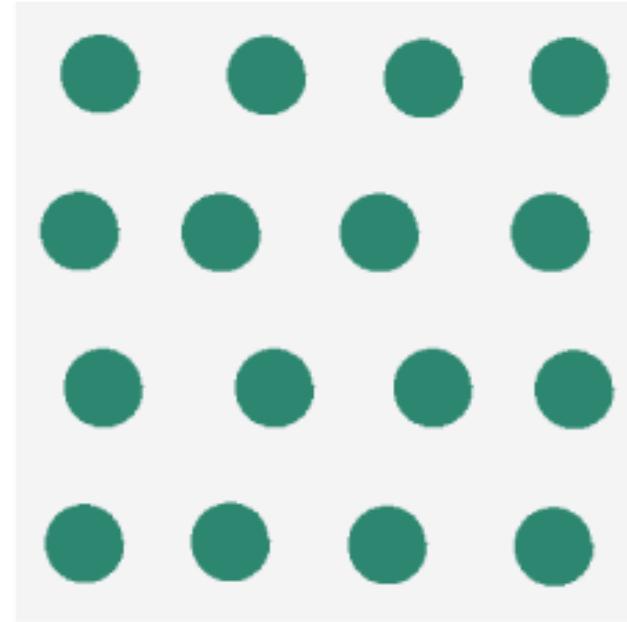
**Long-term equilibrium num. species**



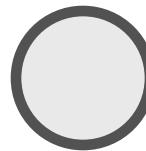
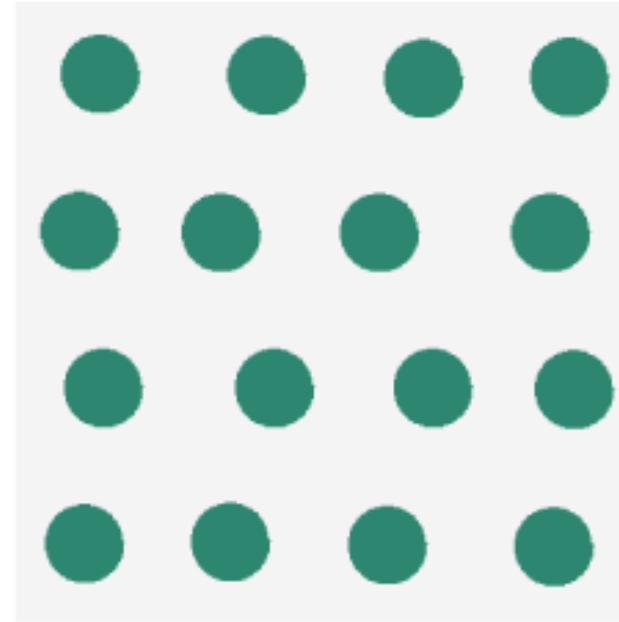
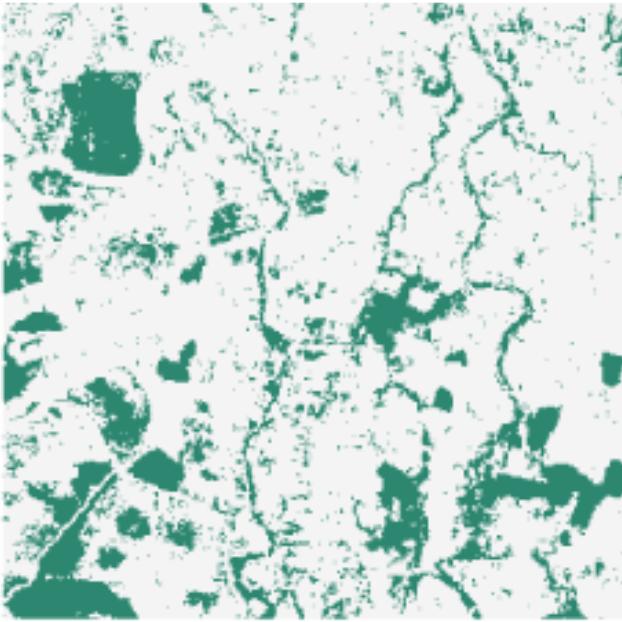
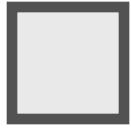
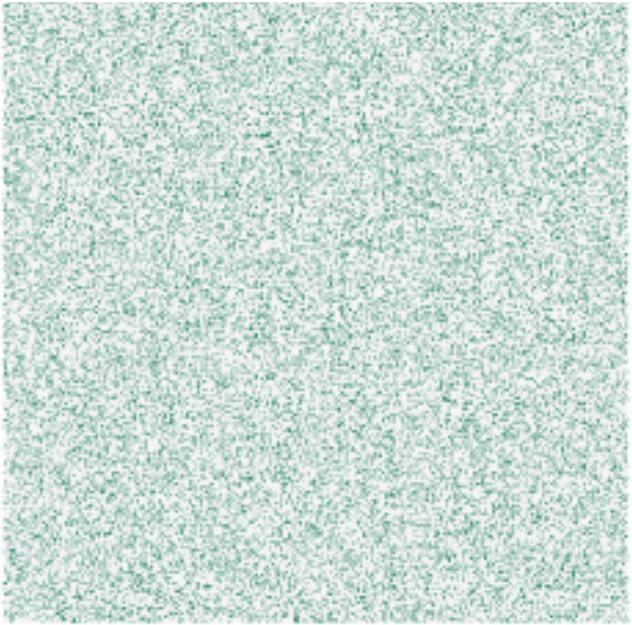
# Audience vote: which is more fragmented?



Fragmentation:  
“breaking or being  
broken into fragments”  
(Oxford Languages)

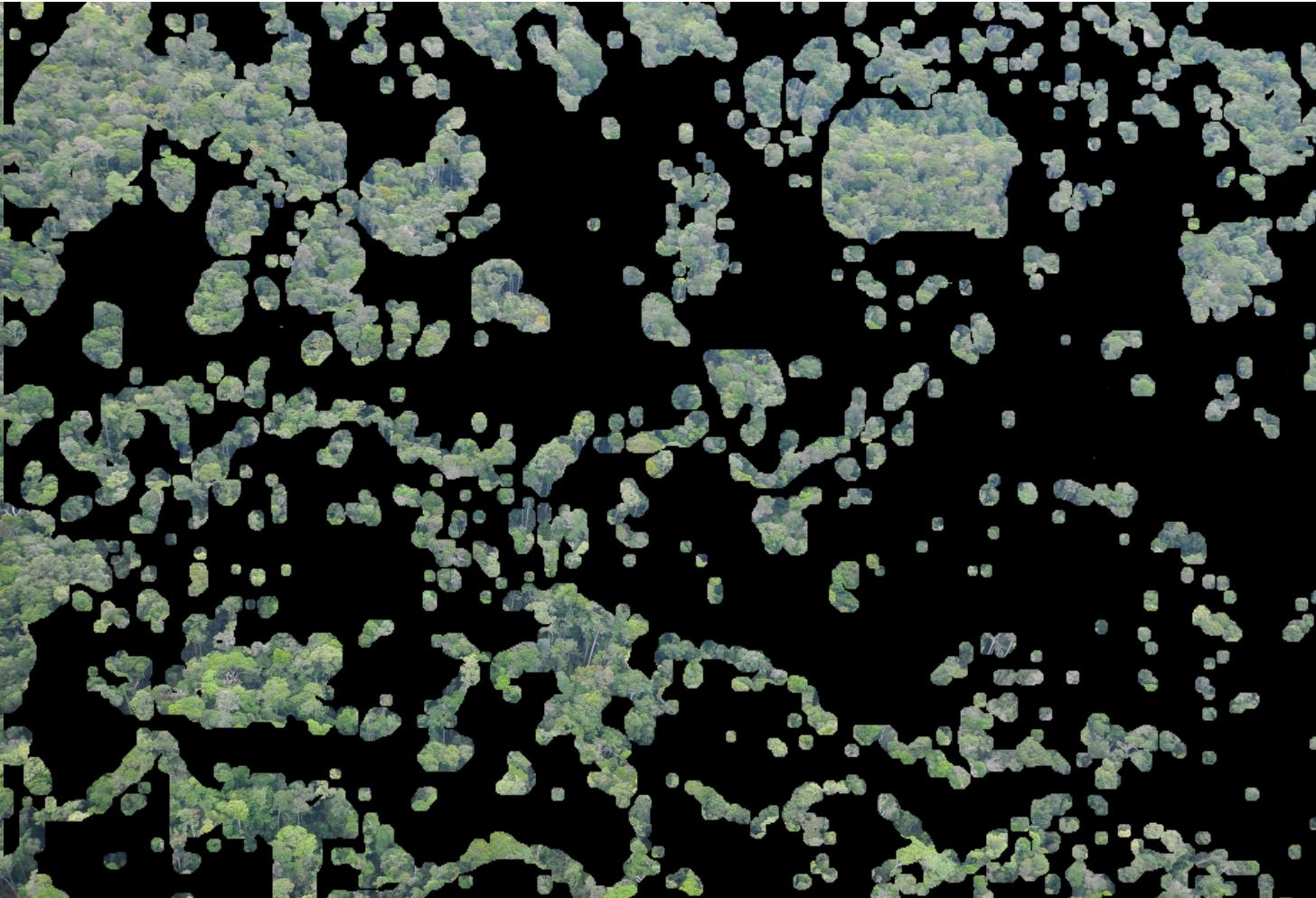


Audience vote:  
which will support more species?



# Effective area $A_e$

Total number of individuals in remaining habitat



**Original num. species**



$$\sigma^2 \Psi\left(\frac{A_{\max}}{\sigma^2}, \nu\right)$$

**Short-term best case num. species**



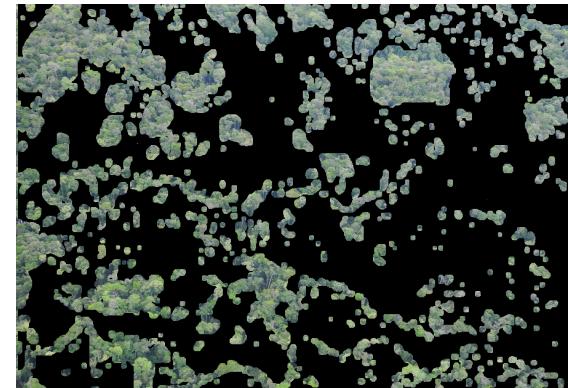
$$\sigma^2 \Psi\left(\frac{A_e}{\sigma^2}, 1 - \left(1 - \nu\right)^{\frac{A_{\max}}{A_e}}\right)$$

**Short-term worst case num. species**



$$\sigma^2 \Psi\left(\frac{A_e}{\sigma^2}, \nu\right)$$

**Long-term equilibrium num. species**

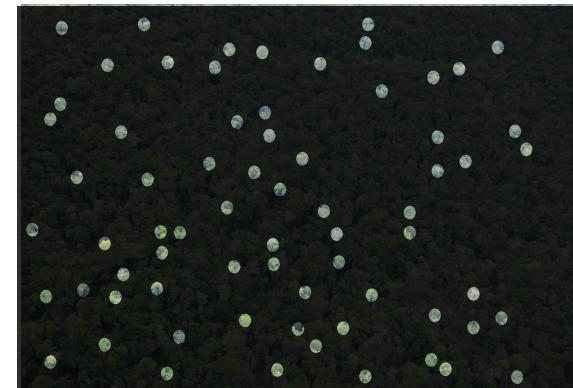


**Original num. species**



$$\sigma^2 \Psi\left(\frac{A_{\max}}{\sigma^2}, \nu\right)$$

**Short-term best case num. species**



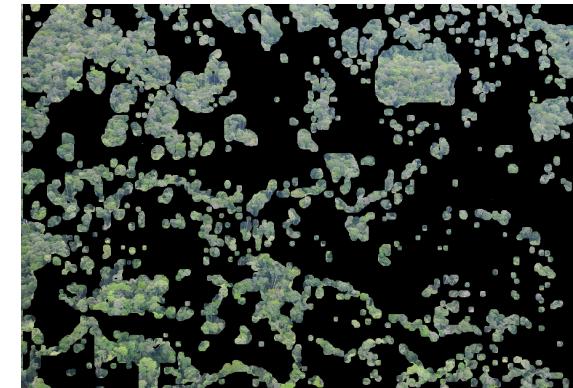
$$\sigma^2 \Psi\left(\frac{A_e}{\sigma^2}, 1 - \left(1 - \nu\right)^{\frac{A_{\max}}{A_e}}\right)$$

**Short-term worst case num. species**



$$\sigma^2 \Psi\left(\frac{A_e}{\sigma^2}, \nu\right)$$

**Long-term equilibrium num. species**

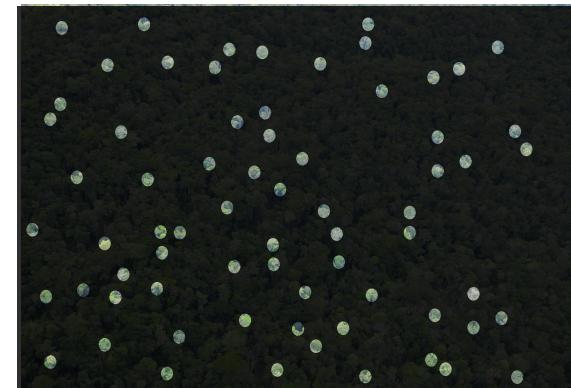


**Original num. species**



$$\sigma^2 \Psi\left(\frac{A_{\max}}{\sigma^2}, \nu\right)$$

**Short-term best case num. species**



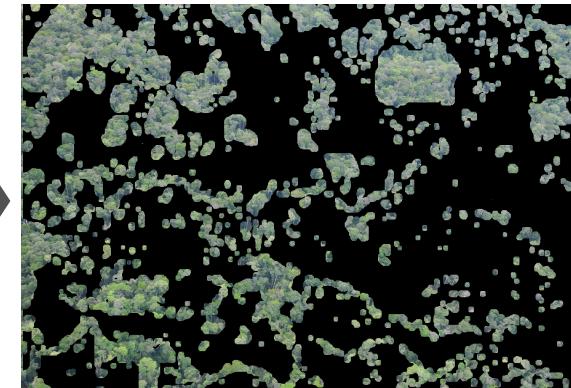
$$\sigma^2 \Psi\left(\frac{A_e}{\sigma^2}, 1 - \left(1 - \nu\right)^{\frac{A_{\max}}{A_e}}\right)$$

**Short-term worst case num. species**



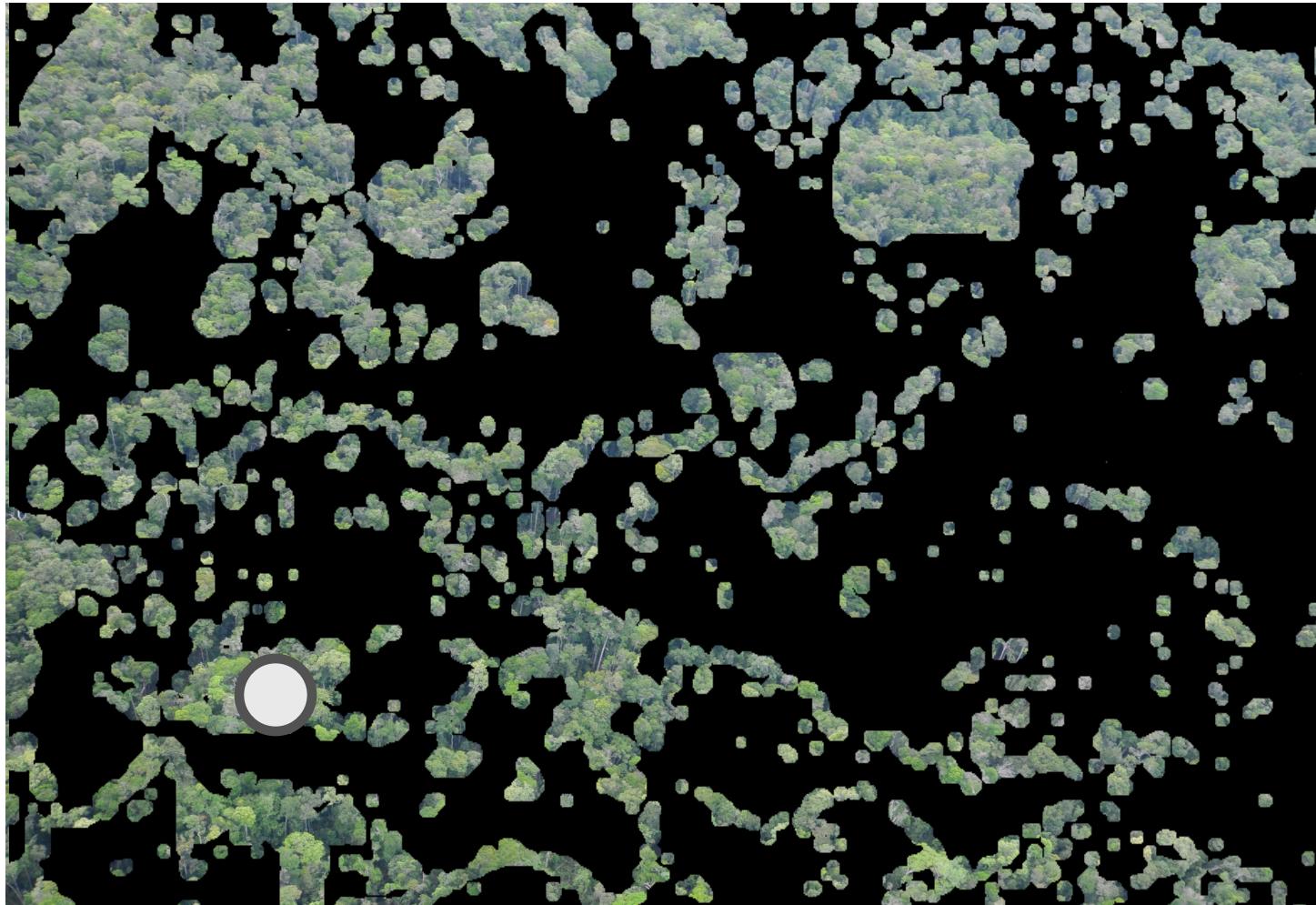
$$\sigma^2 \Psi\left(\frac{A_e}{\sigma^2}, \nu\right)$$

**Long-term equilibrium num. species**



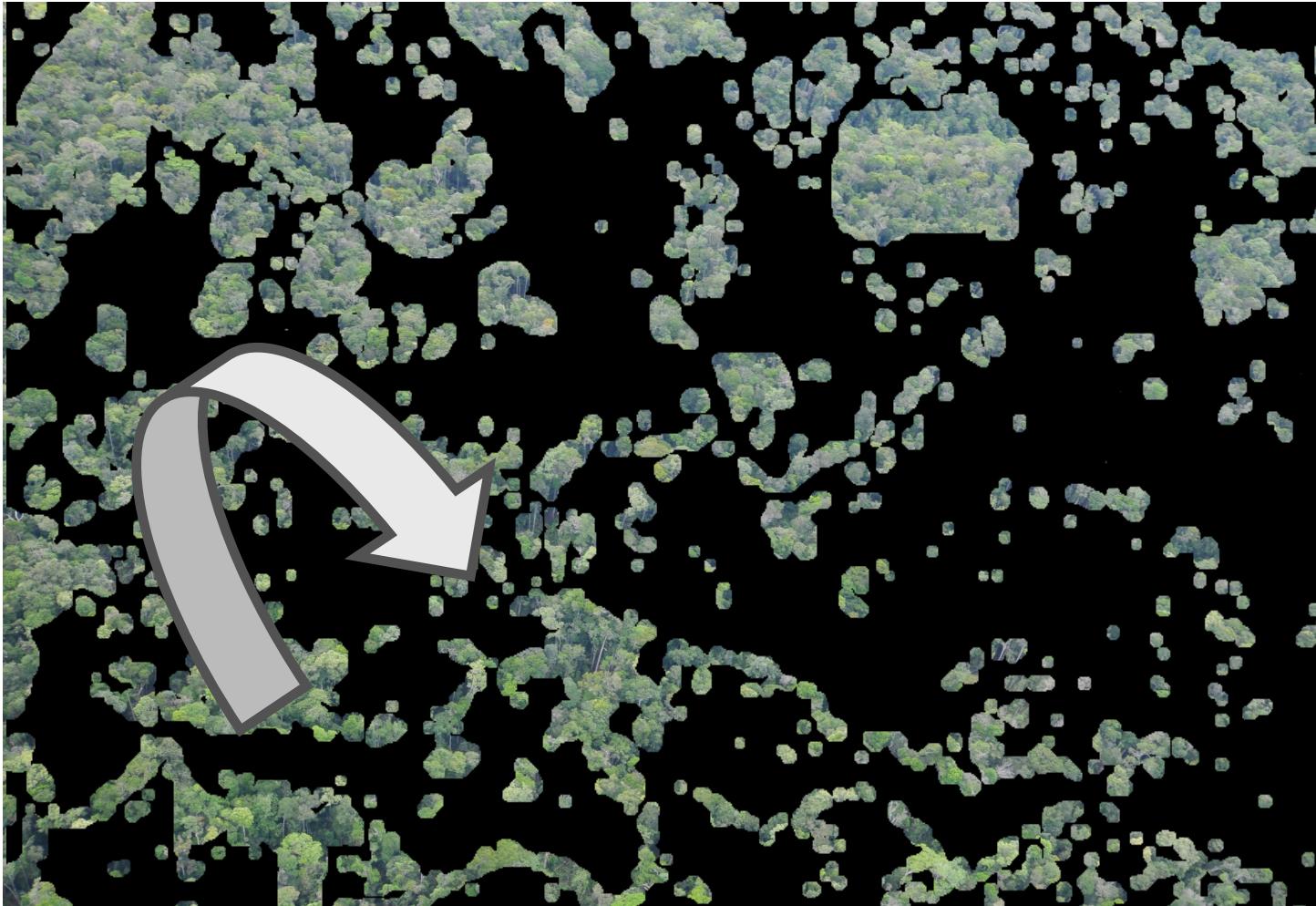
# Effective connectivity $C_e$ (of a cell)

Squared mean dispersal per hop  
over multiple hops starting in the cell



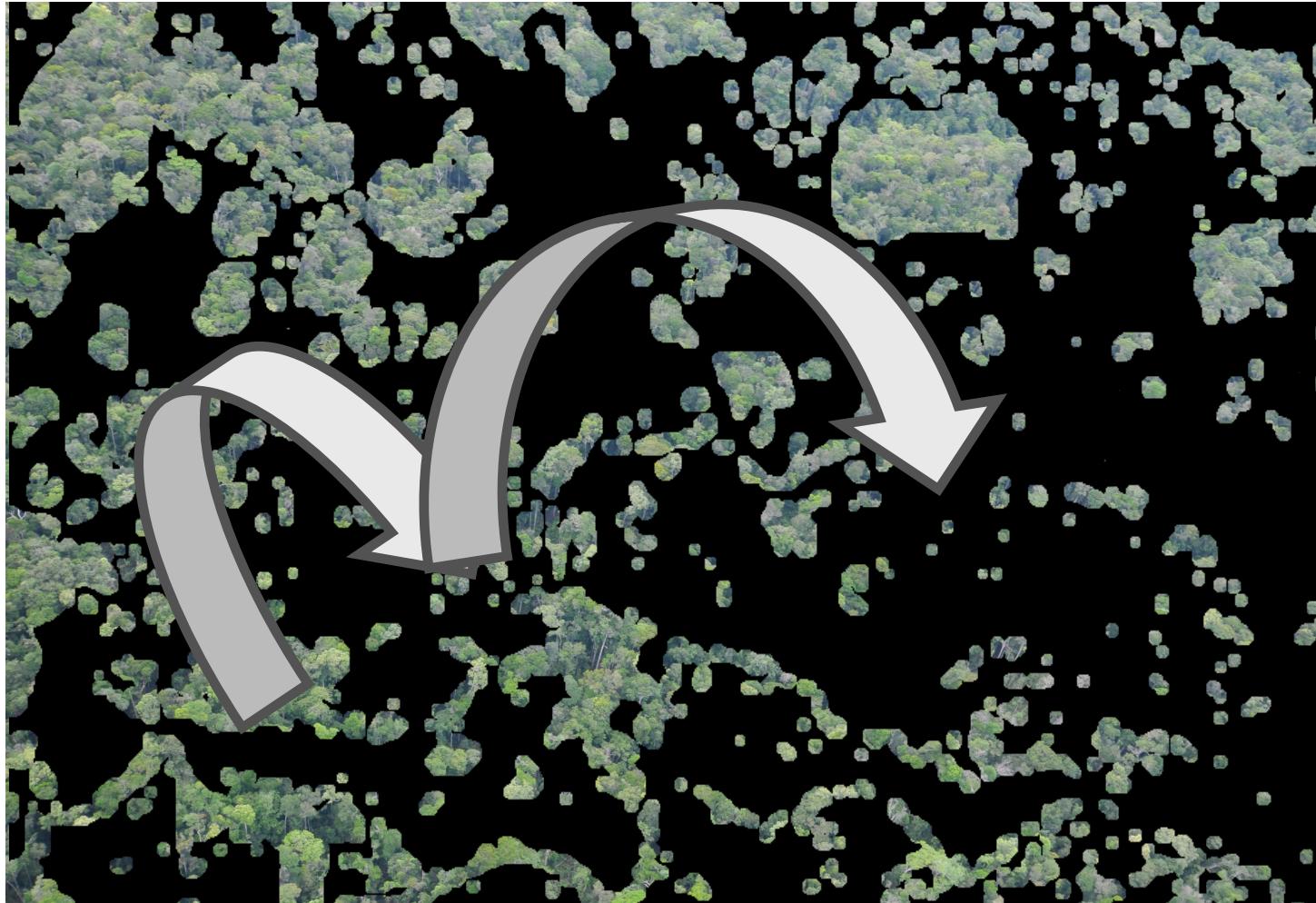
# Effective connectivity $C_e$ (of a cell)

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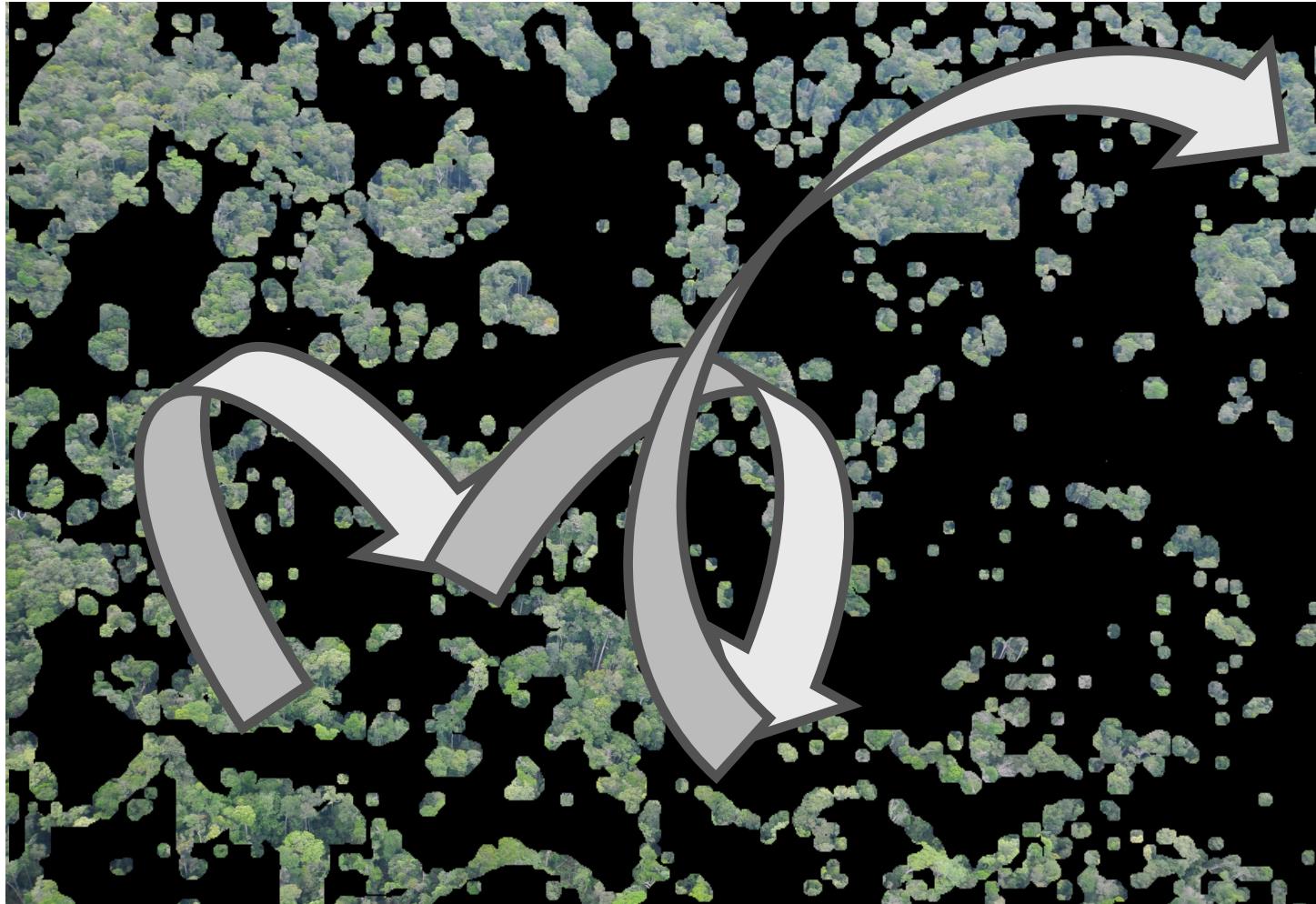
# Effective connectivity $C_e$ (of a cell)

Squared mean dispersal per hop  
over multiple hops starting in the cell



# Effective connectivity $C_e$ (of a cell)

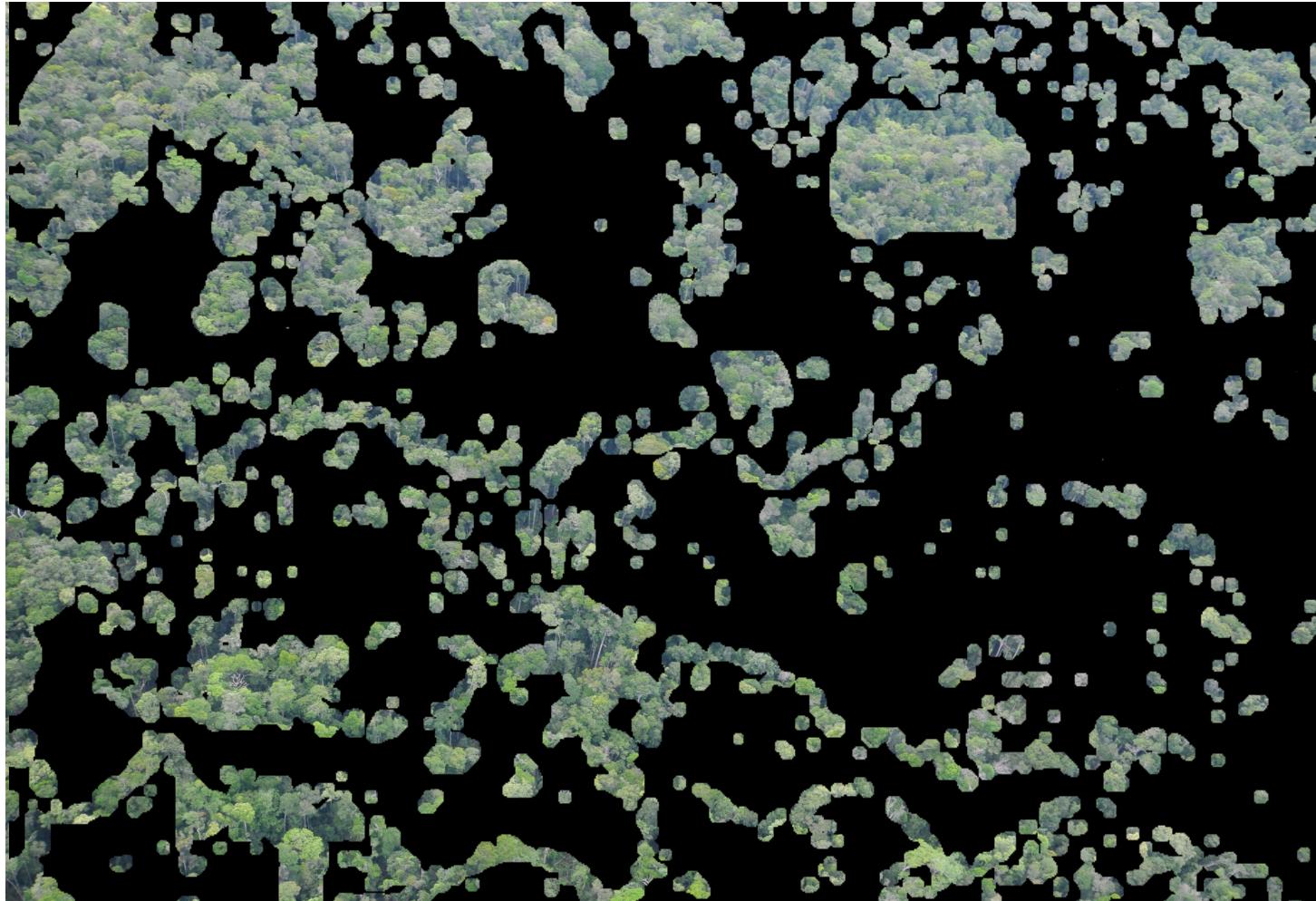
Squared mean dispersal per hop  
over multiple hops starting in the cell



# Effective connectivity $C_e$

Mean effective connectivity of all cells

(cells with no habitat get connectivity = 0)

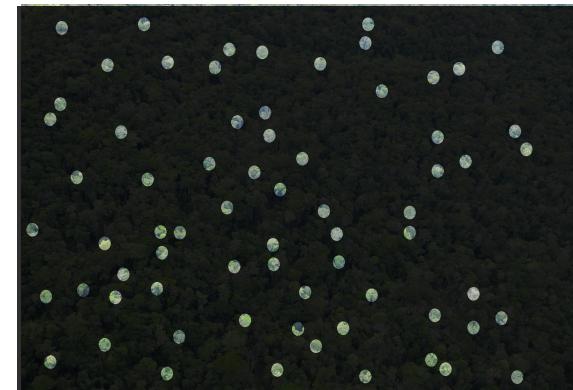


**Original num. species**



$$\sigma^2 \Psi\left(\frac{A_{\max}}{\sigma^2}, \nu\right)$$

**Short-term best case num. species**



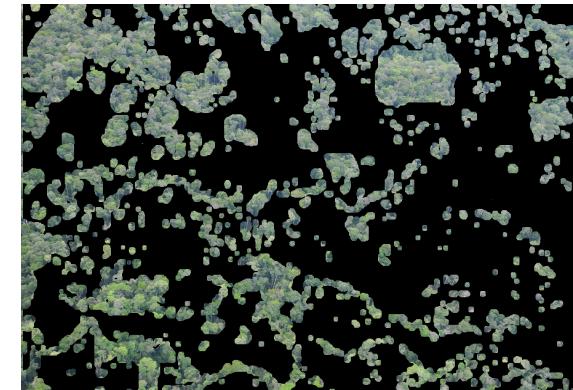
$$\sigma^2 \Psi\left(\frac{A_e}{\sigma^2}, 1 - \left(1 - \nu\right)^{\frac{A_{\max}}{A_e}}\right)$$

**Short-term worst case num. species**

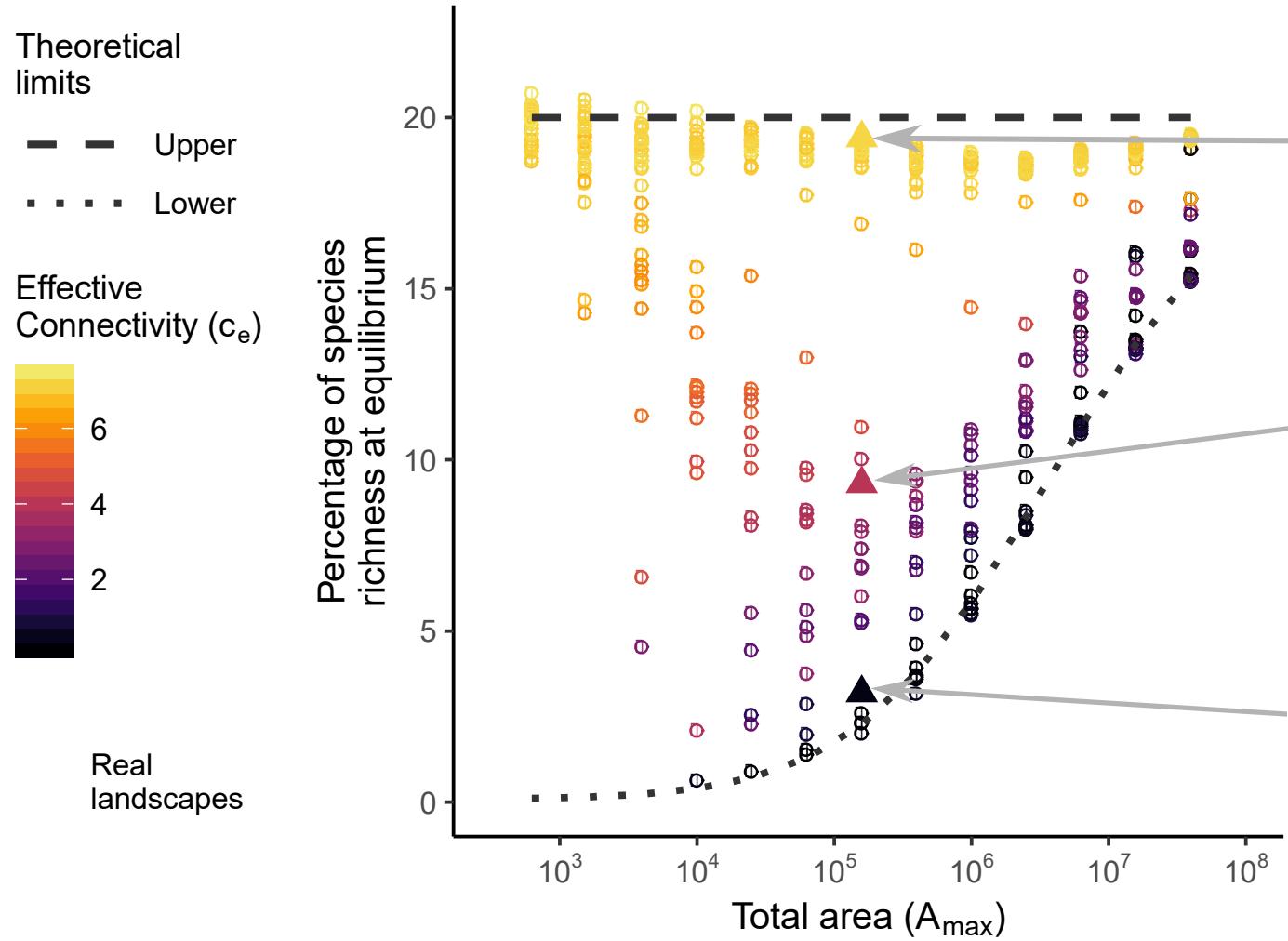


$$\sigma^2 \Psi\left(\frac{A_e}{\sigma^2}, \nu\right)$$

**Long-term equilibrium num. species**



$$C_e^2 \Psi\left(\frac{A_e}{C_e^2}, \nu\right)$$



Theoretical  
limits

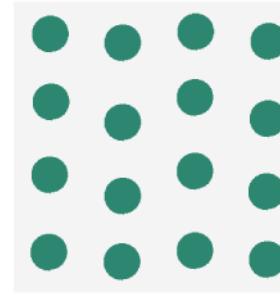
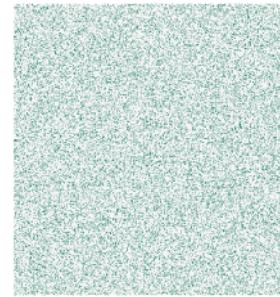
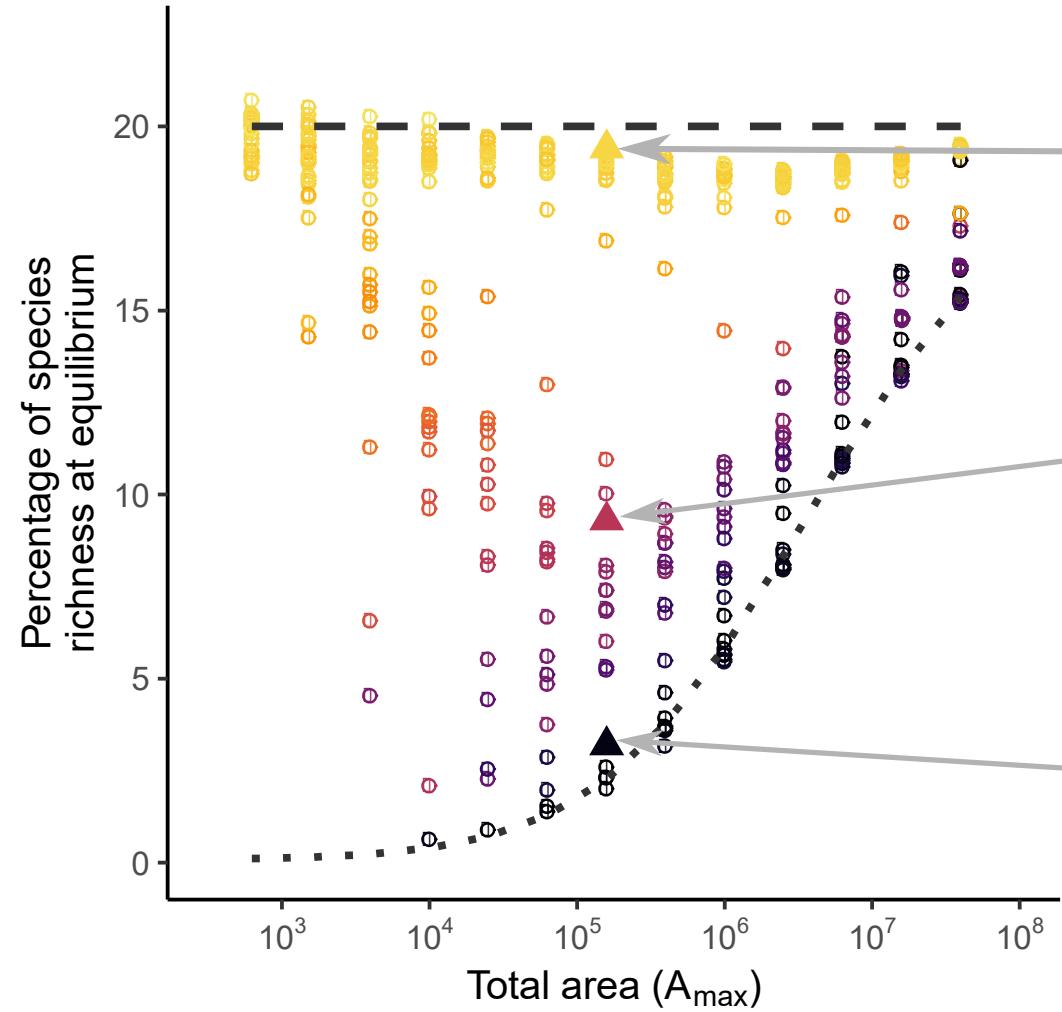
— — Upper

· · · Lower

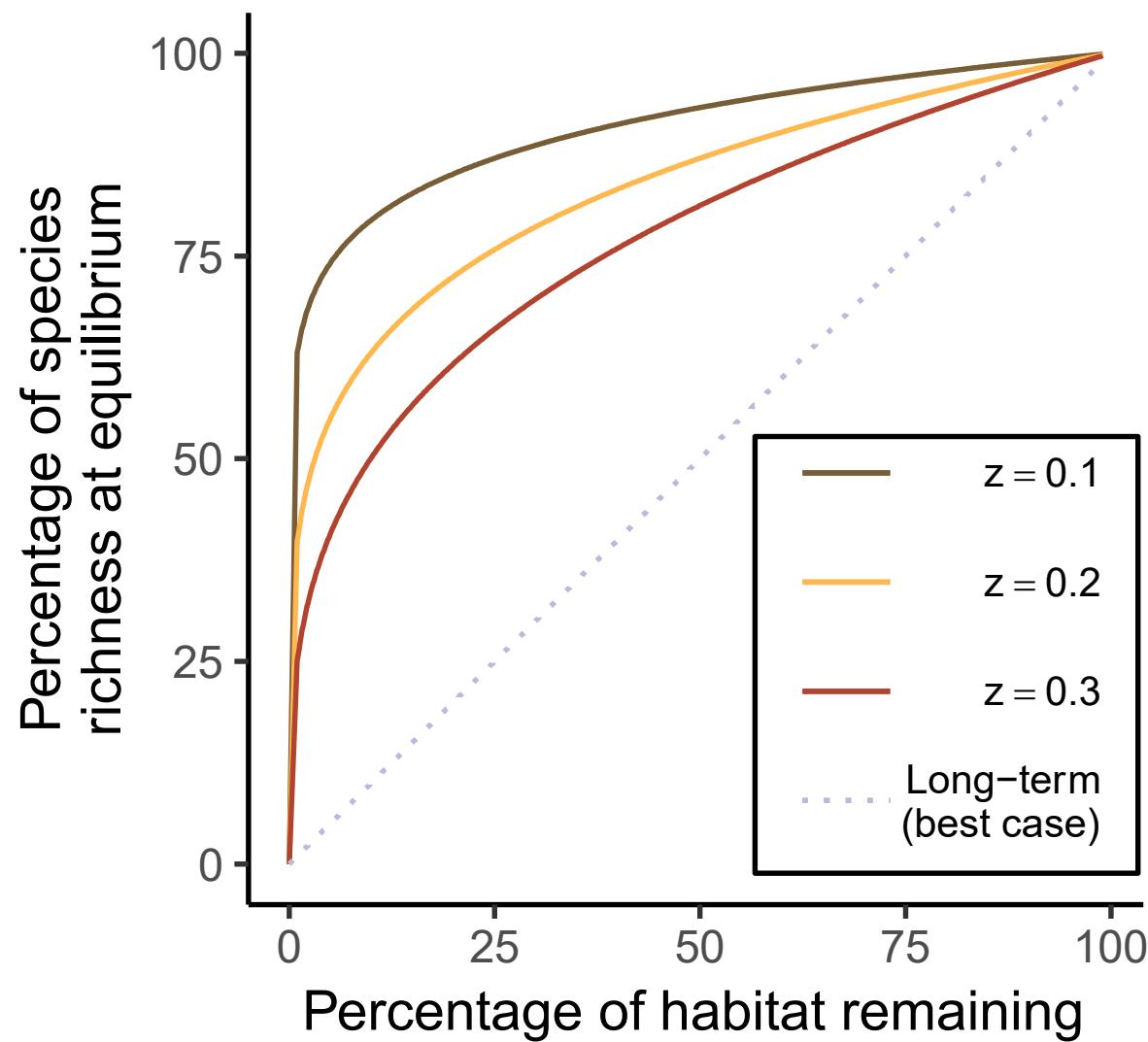
Effective  
Connectivity ( $c_e$ )



Real  
landscapes

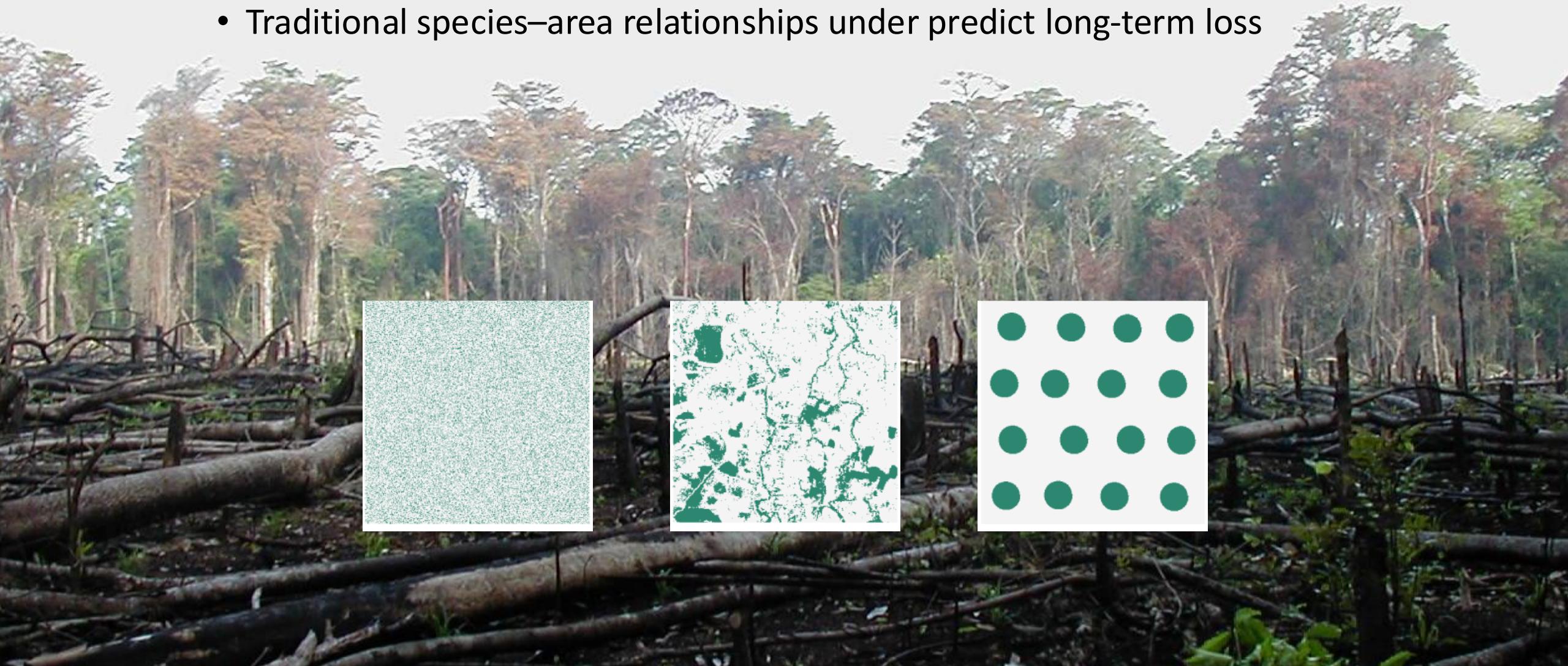


## Power law approach vs long-term Preston function (best case)



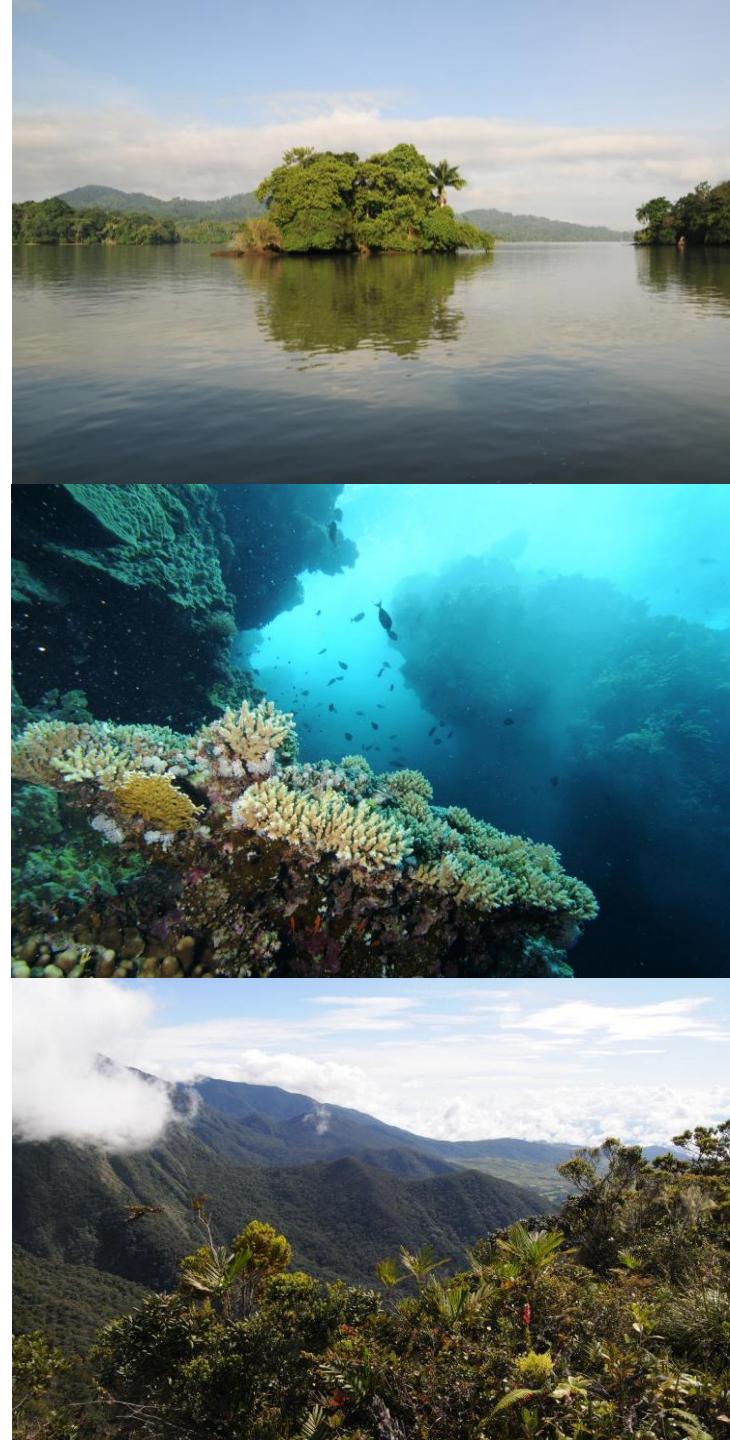
# How many species will go extinct in response to loss of habitat?

- Formulas for short (best and worst case) and long term
- Effective area and effective connectivity matter in the long term
- Traditional species-area relationships under predict long-term loss



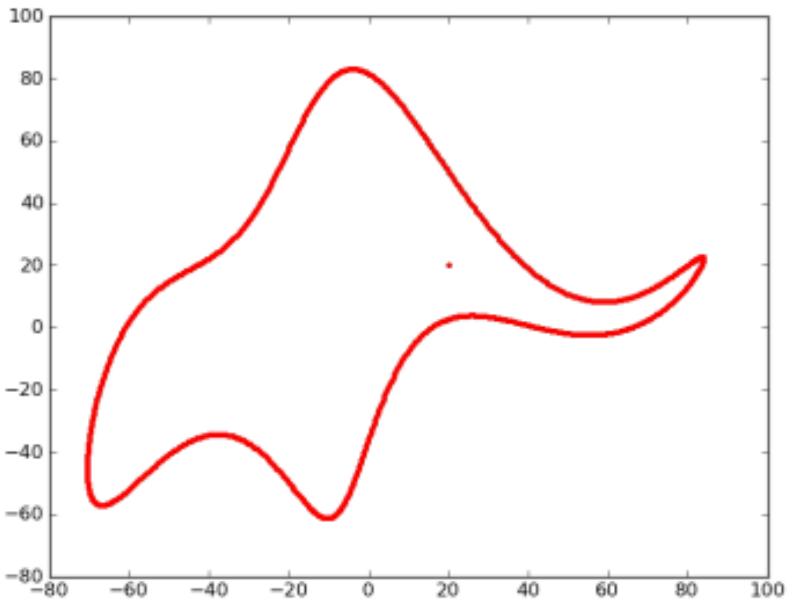
# What have we learned about modeling

- John von Neumann “Give me four parameters, and I can fit an elephant. Give me five, and I can wiggle its trunk”.

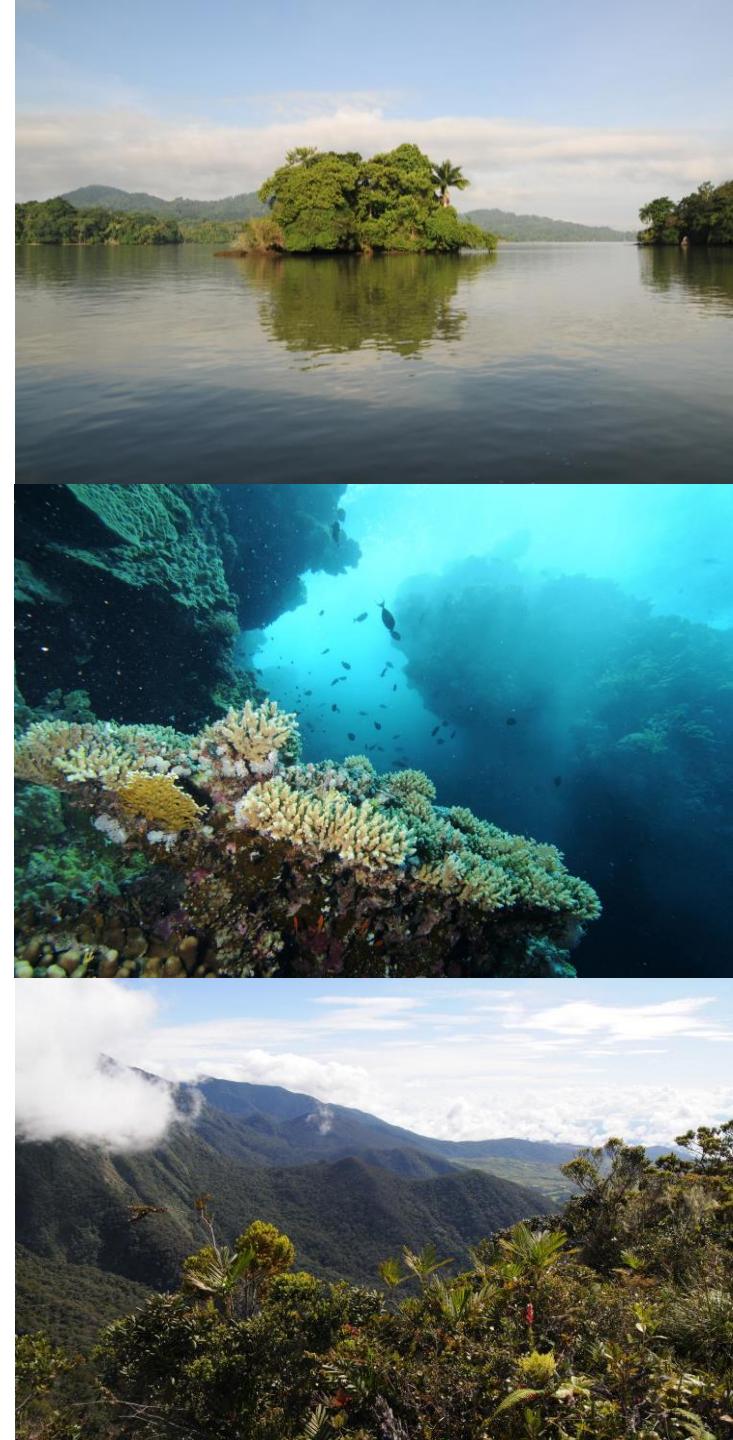


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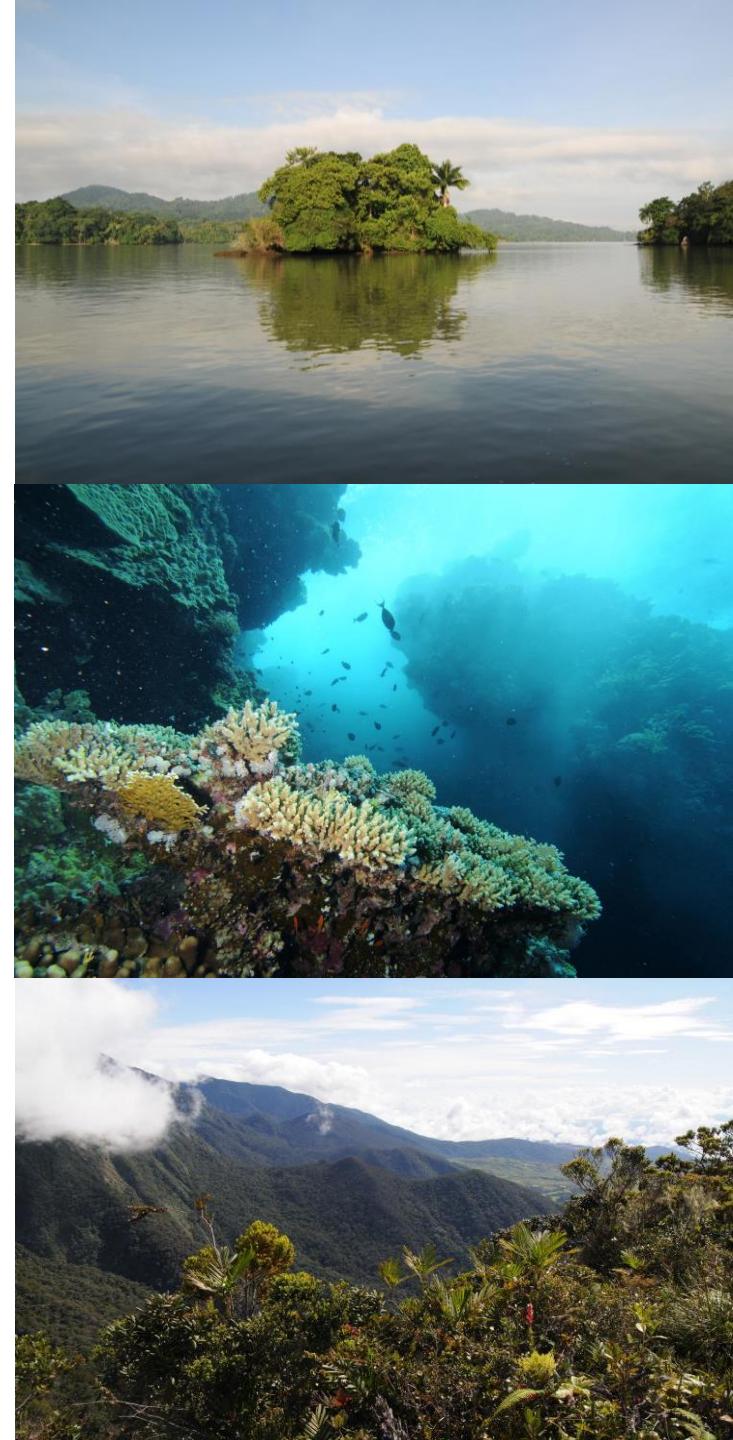


Mayer, Khaled Khairy, and Jonathon Howard (2010). “Drawing an elephant with four complex parameters”, Am. J. Phys. 78, 648, DOI:10.1119/1.3254017.



# What we have learned about modelling

- John von Neumann “Give me four parameters, and I can fit an elephant. Give me five, and I can wiggle its trunk”.
- Theories in biology and in physics are very different
- Modelling for making predictions, and for gaining understanding are two different types of exercise
- Not all data are very informative
- Simplicity vs. complexity – only add complexity when it's needed, use computers when needed
- Start with the end in mind



# Neutral theory conclusions

- Neutral theory is a collection of neutral models assuming the demographic properties of an individual are independent of its species identity
- Useful for understanding and predicting but not both at the same time.
- Explains species area relationships and other spatial biodiversity patterns.
- Makes rich predictions about biodiversity and endemicity on islands.
- Neutral theory is one of the many useful tools you have in your tool box.

