Coupled metapopulation dynamics with patch modification and memory

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Ecosystem engineering everywhere

- All organisms modify their environment, and react to environmental state

- Environmental modification mediates interactions in many communities

- Classical ecological theory studies some special cases (e.g. resource competition), usually *locally*

- **What do community dynamics look like on the landscape scale?**

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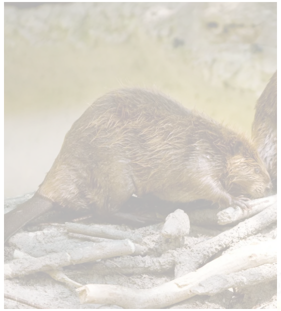

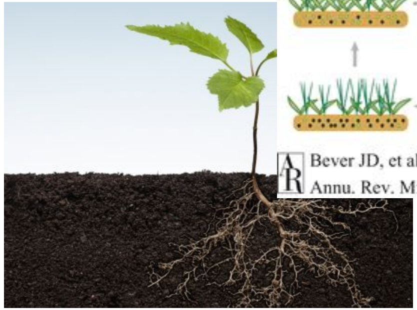

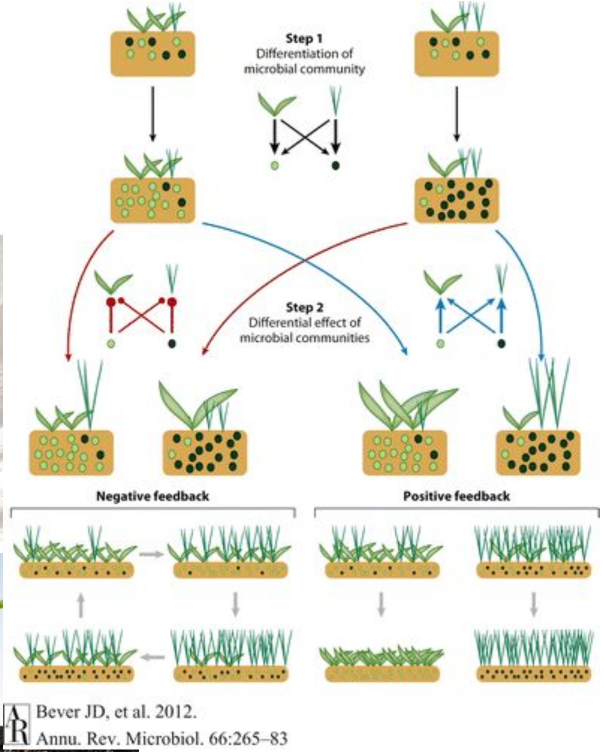

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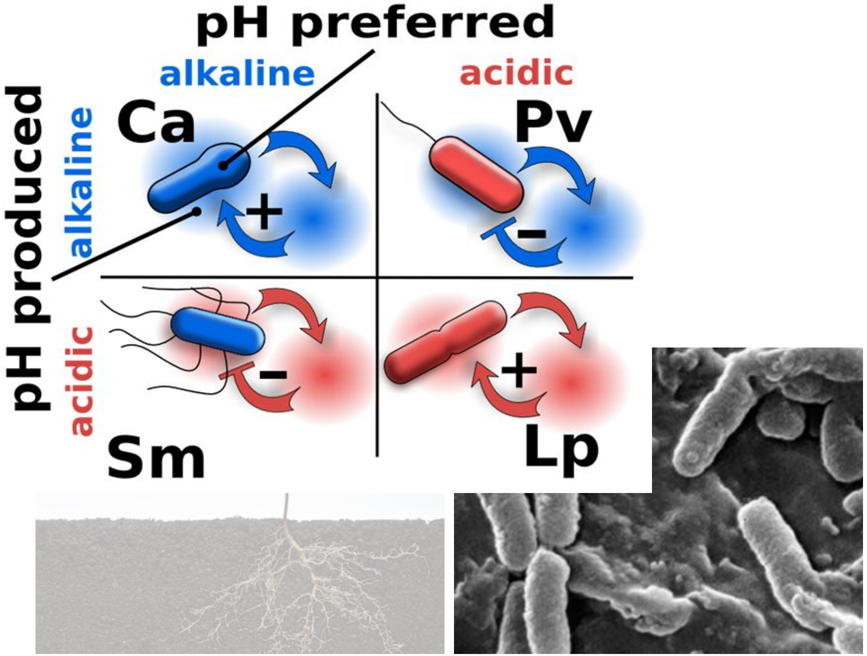

Ratzke and Gore. PLOS Bio (2018)

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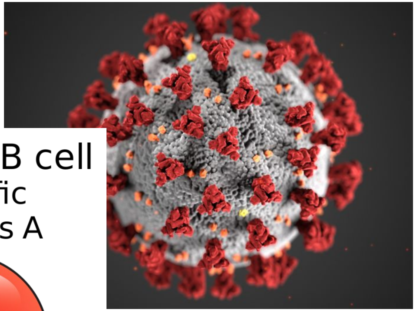

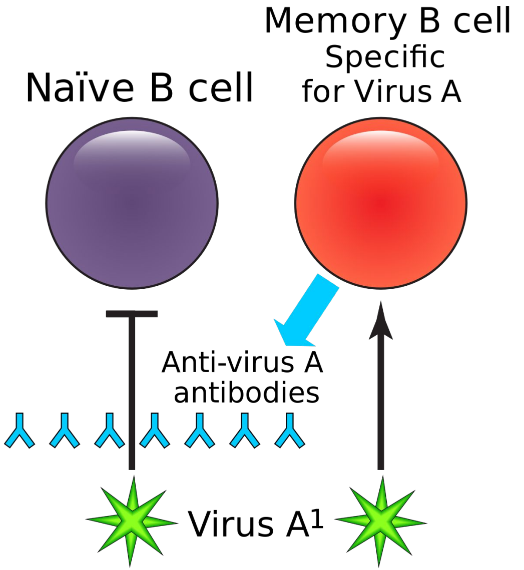

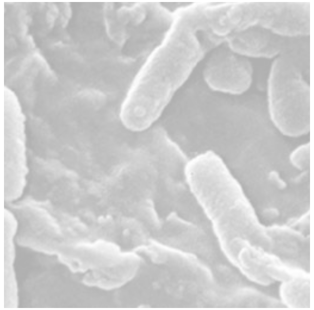

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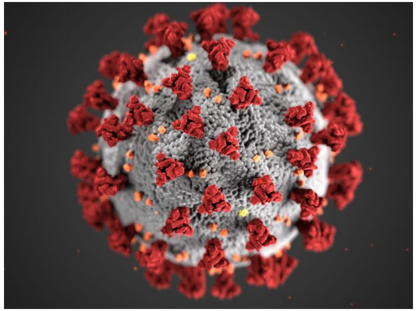
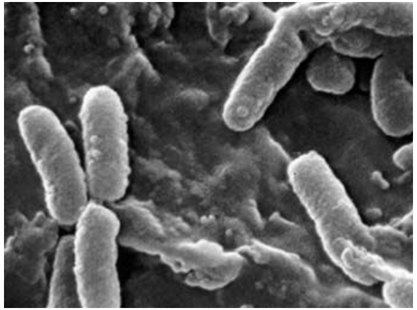
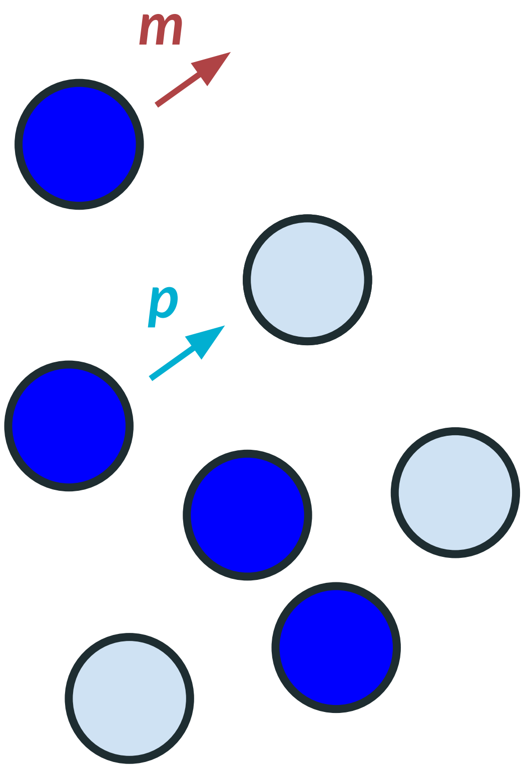




Metapopulation models

Levins (1969) introduced a simple model for **migration** and **extinction** in a landscape:

$$\frac{dx}{dt} = -\underset{\substack{\uparrow \\ \text{Extinction} \\ \text{rate}}}{m}\,\underset{\substack{\uparrow \\ \text{Fraction} \\ \text{occupied}}}{x} + \underset{\substack{\uparrow \\ \text{Colonization} \\ \text{rate}}}{p}\,x\,\underbrace{(1 - x)}_{\substack{\text{Fraction} \\ \text{unoccupied}}}$$



Metapopulation models

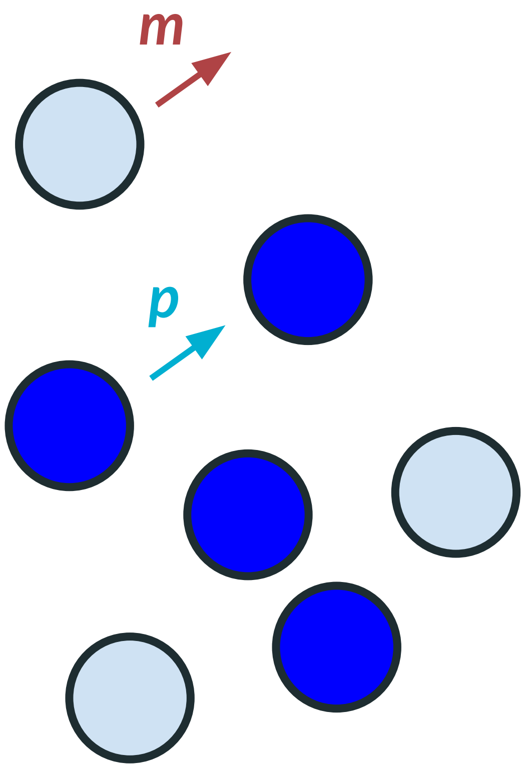
Levins (1969) introduced a simple model for migration and extinction in a landscape:

$$\frac{dx}{dt} = -m\,x + p\,x\,(1 - x)$$

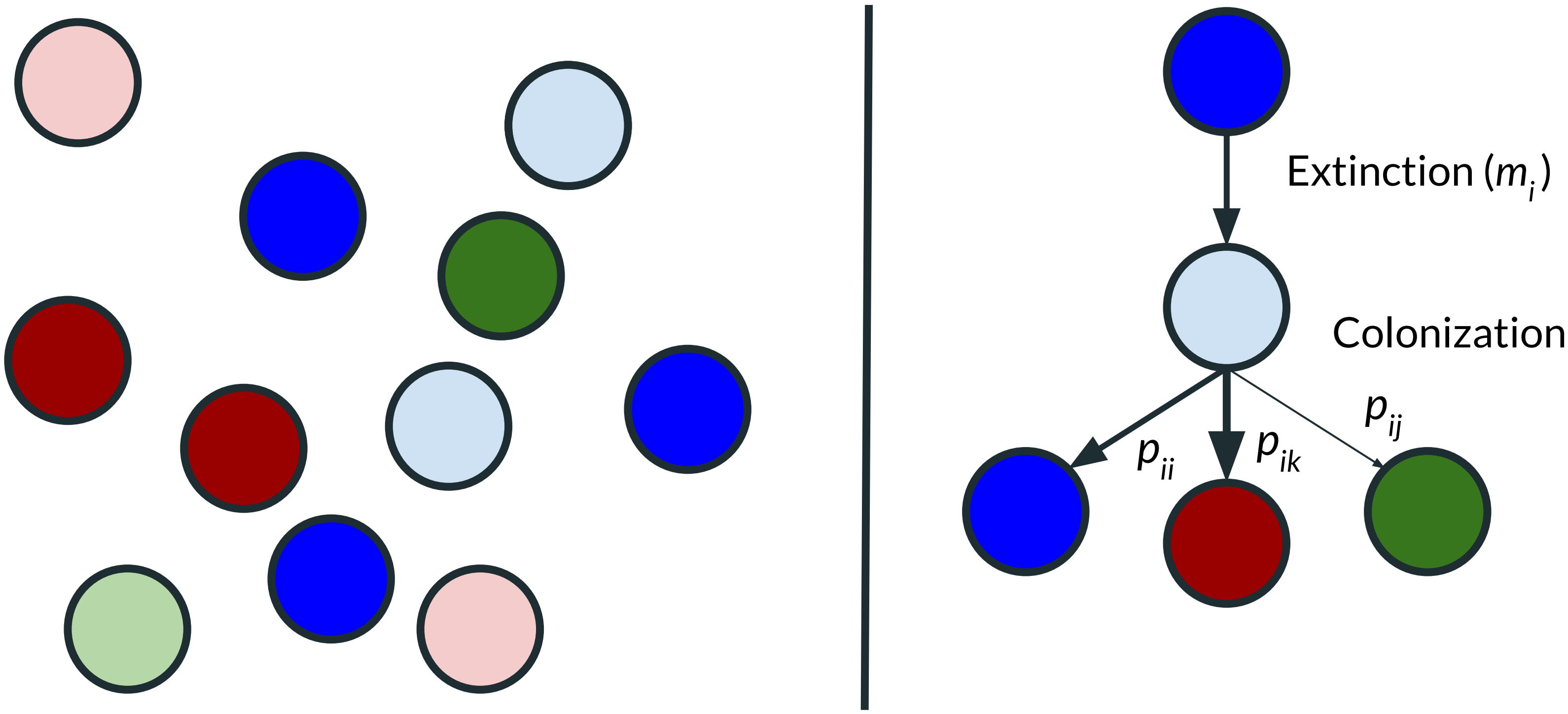
An equivalent (SIS-like) description:

$$\frac{dx}{dt} = -m\,x + p\,x\,y$$

$$\frac{dy}{dt} = m\,x - p\,x\,y$$

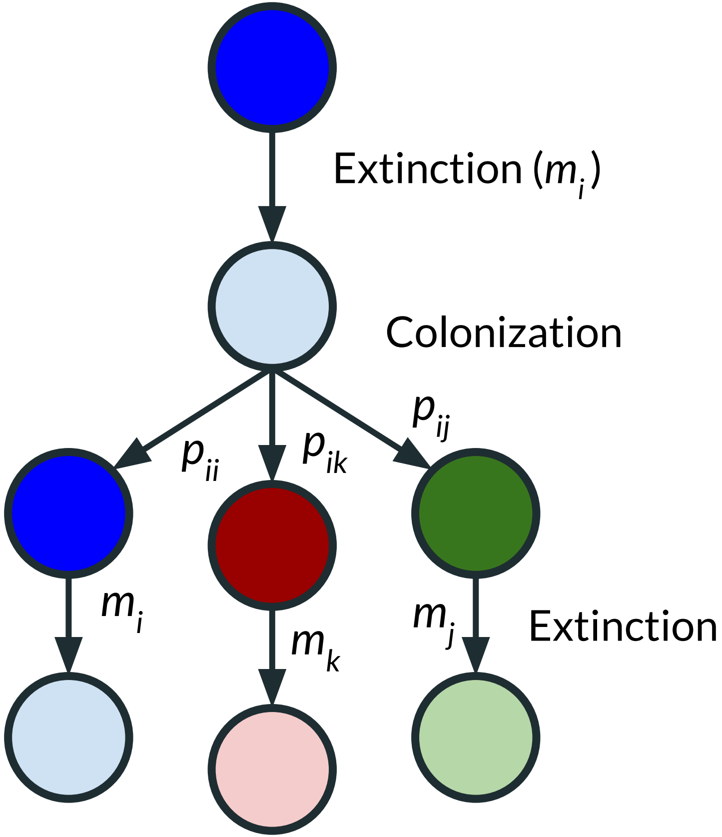


Patch modification and memory



Patch modification and memory

- Patch modification is incorporated implicitly, through state-specific colonization probabilities (p_{ij})
- Patch state depends on the last occupant only
- Patch “memory” is permanent until re-set by new colonizer
- Extinction/mortality rates (m_i) are species-specific, and insensitive to patch state



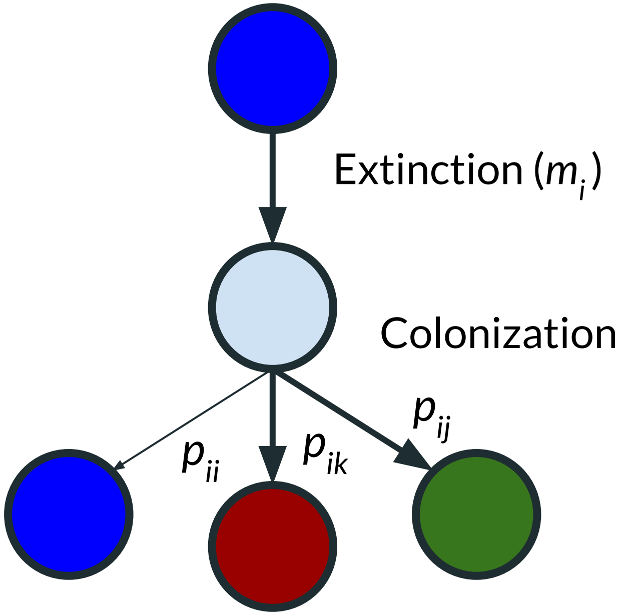
Patch modification and memory

Local extinction

Colonization

$$\frac{dx_i}{dt} = -m_i\, x_i + x_i \sum_j p_{ij}\, y_j$$

$$\frac{dy_i}{dt} = m_i\, x_i - y_i \sum_j p_{ji}\, x_j$$



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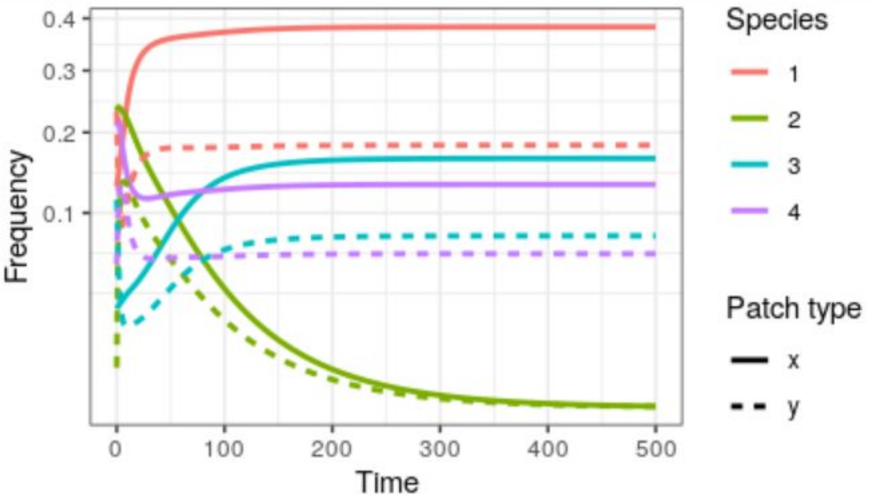

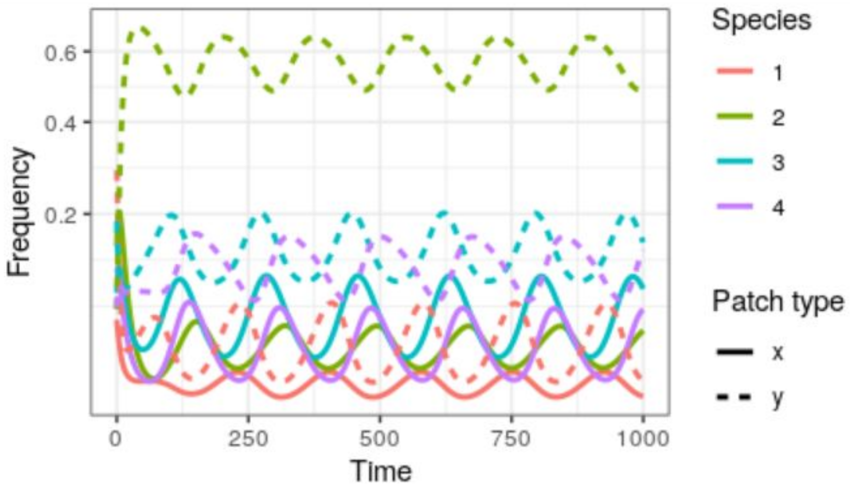

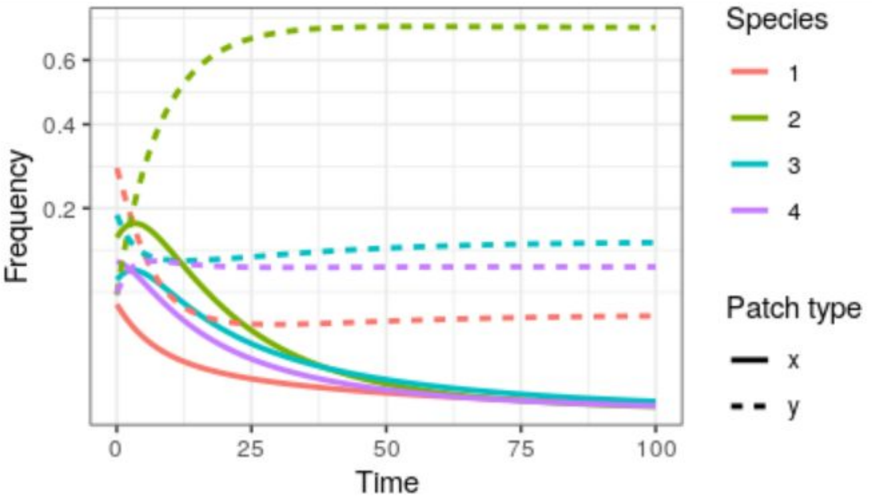

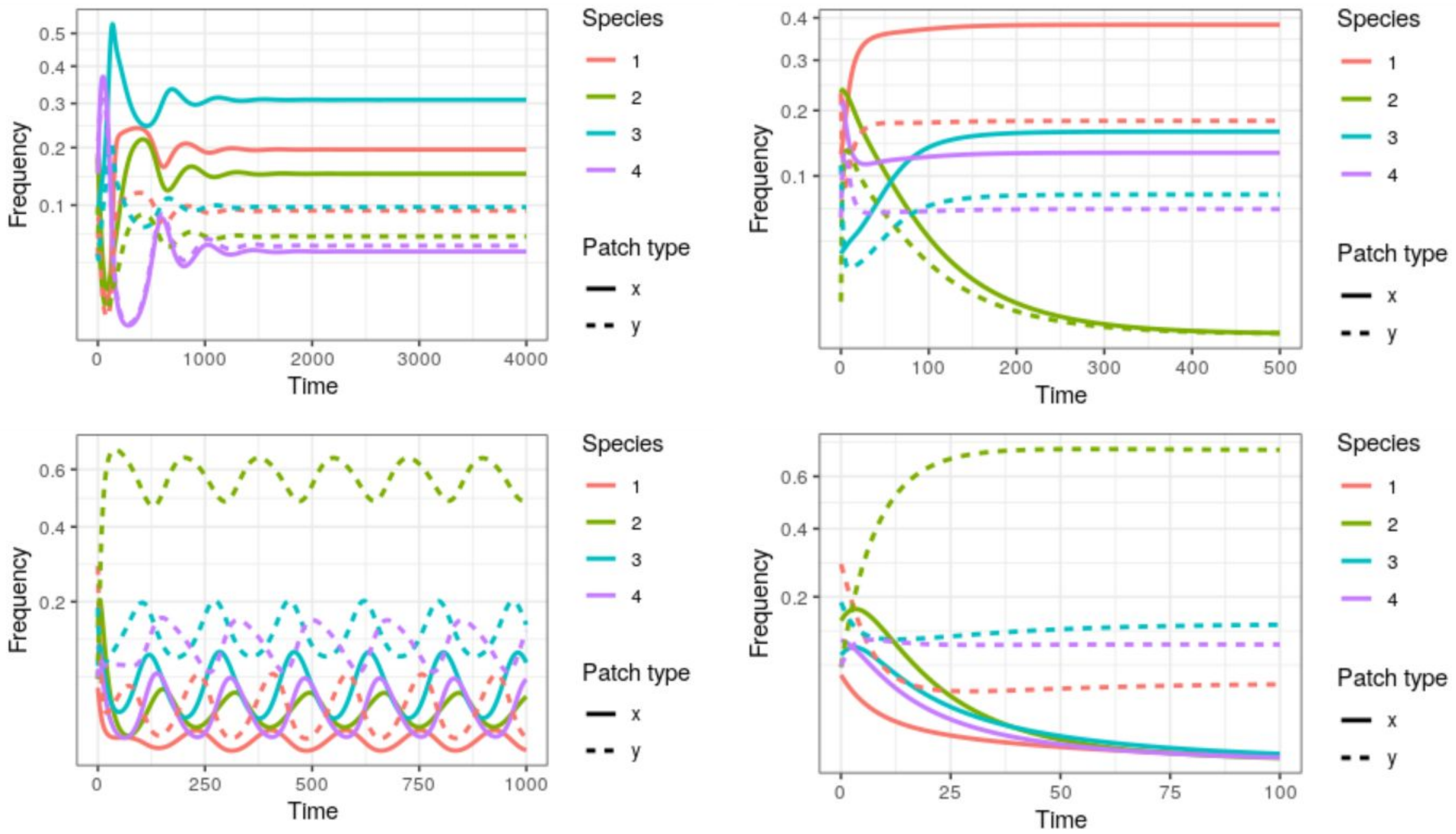

Frequency
Time
Species
1
2
3
4
Patch type
x
y
0.5
0.4
0.3
0.2
0.1
0
1000
2000
3000
4000
0.4
0.3
0.2
0.1
0
100
200
300
400
500
0.6
0.4
0.2
0
250
500
750
1000
0.6
0.4
0.2
0
25
50
75
100

Long-term dynamics

Existing literature focuses on positive vs. negative feedbacks:

Patches last occupied by a conspecific might have:

- Suitable abiotic conditions (e.g. pH, fire)
- Symbionts / mutualists present
- Immunodeficiency or antibody-dependent enhancement

...but also

- Depleted or degraded resources / environment
- Specific predators / parasites/ pathogens present
- Specific immunity

Positive feedbacks should be destabilizing, while negative feedbacks should be stabilizing (enhance coexistence)

Long-term dynamics: The simplest case

A minimal model where $m_i = m$, and p_{ij} depends only on $i = i$ or $i \neq j$

$$P = \alpha I + \beta 11^T = \begin{pmatrix} \alpha+\beta & \beta & \beta & \cdots \\ \beta & \alpha+\beta & \beta & \cdots \\ \beta & \beta & \alpha+\beta & \cdots \\ \vdots & \vdots & \vdots & \ddots \end{pmatrix}$$

$$y^* = \frac{m}{\alpha+\beta\, n}$$

$$x^* = \frac{1}{n} - y^*$$

Feasibility requires:

$$m < \beta + \frac{\alpha}{n}$$

Long-term dynamics: The simplest case

$$P = \alpha I + \beta 11^T$$

- When will the system approach the *n*-species equilibrium?

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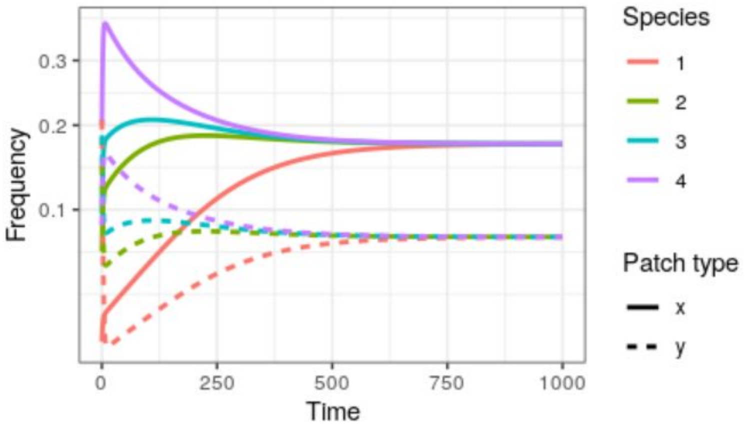
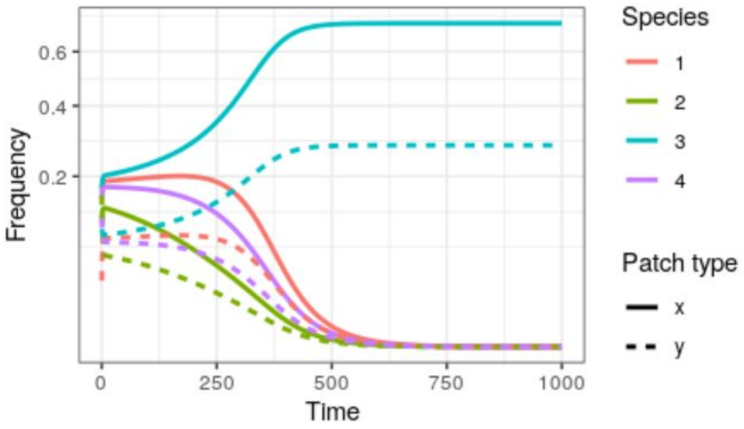
- Consistent with our intuition, negative feedbacks maintain diversity when $\alpha < 0$ and positive feedbacks diminish it when $\alpha > 0$





Long-term dynamics: The simplest case

$$P = \alpha I + \beta 1 1^T$$

- When will the system approach the *n*-species equilibrium?
- Consistent with our intuition, negative feedbacks maintain diversity when $\alpha < 0$ and positive feedbacks diminish it when $\alpha > 0$
- Using an embedding technique from dynamical systems theory, we can prove that the coexistence equilibrium is globally stable for $\alpha < 0$
- Demographic differences between species (i.e. $m_i \neq m_j$ and/or $\alpha_i \neq \alpha_j$) never affect stability

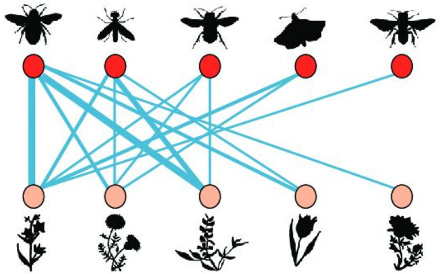
<u>Key question:</u> How do we generalize the idea that stable coexistence occurs whenever conspecifics have a disadvantage recolonizing patches?

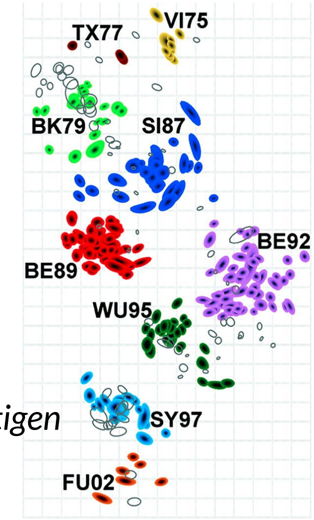
Arbitrary symmetric P

$$p_{ij} = p_{ji}$$

- When $m_i = m$, we can perform local stability analysis for any number of species

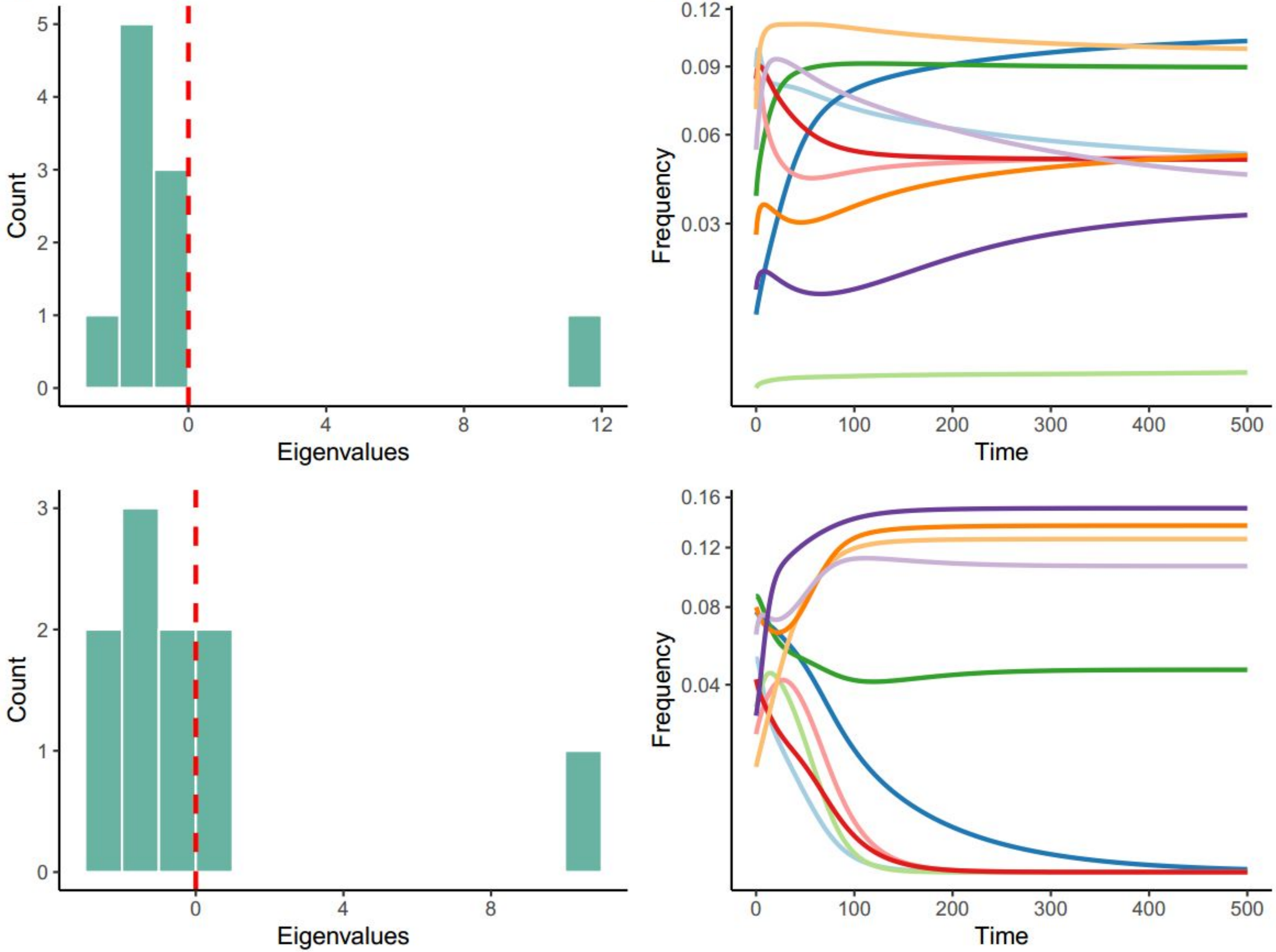
- The coexistence equilibrium is stable if and only if P has **exactly 1 positive eigenvalue**





Distances between flu strains in antigen space

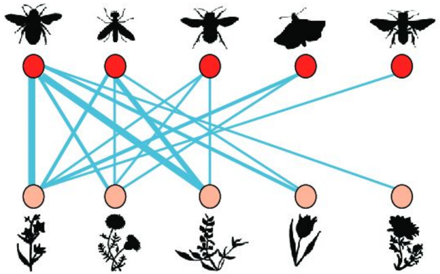
Frost et al. TREE (2019)
modified from Smith et al. Science (2004)

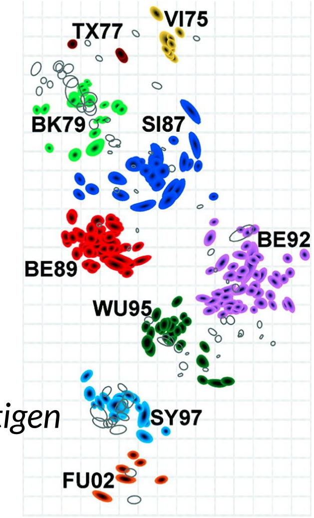


Count
Eigenvalues
0
4
8
12
0
1
2
3
4
5
Frequency
Time
0.12
0.09
0.06
0.03
0
100
200
300
400
500
Count
Eigenvalues
0
4
8
0
1
2
3
Frequency
Time
0.16
0.12
0.08
0.04
0
100
200
300
400
500

Arbitrary symmetric P

- When $m_i = m$, we can perform local stability analysis for any number of species
- The coexistence equilibrium is stable if and only if *P* has **exactly 1 positive eigenvalue**
- Numerical evidence indicates that this condition is also sufficient for global stability, unaffected by variation in m_i
- A *necessary* condition is $p_{ij} > \min(p_{ii}, p_{jj})$
- Eigenvalue condition generalizes the intuitive notion of **“negative feedbacks”** to complex communities





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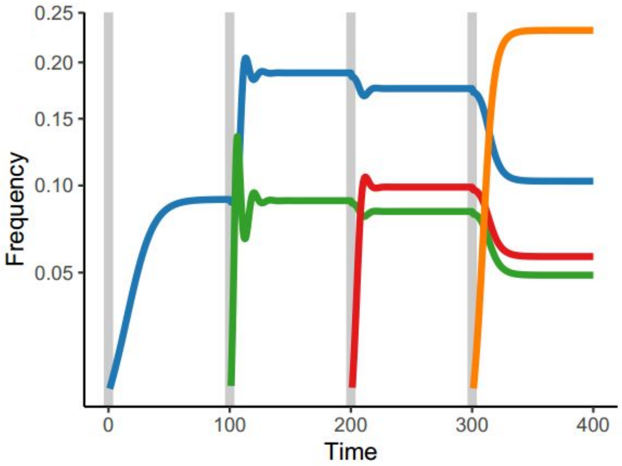
Coexistence induces a positive diversity-robustness relationship

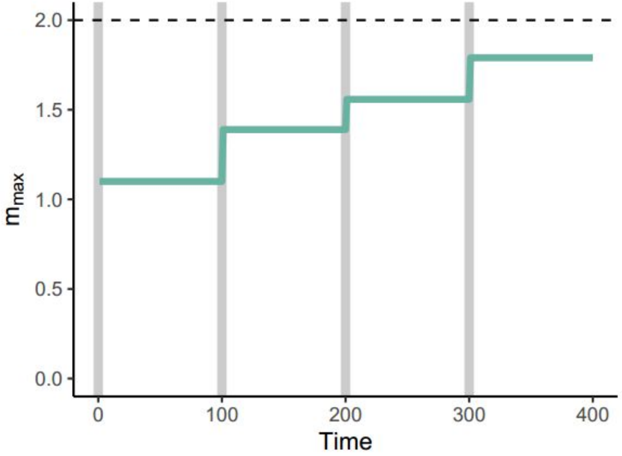
- More diverse communities can tolerate higher local extinction rates
    - e.g. more disturbance, lower environmental quality, etc.

Recalling the simplest model....

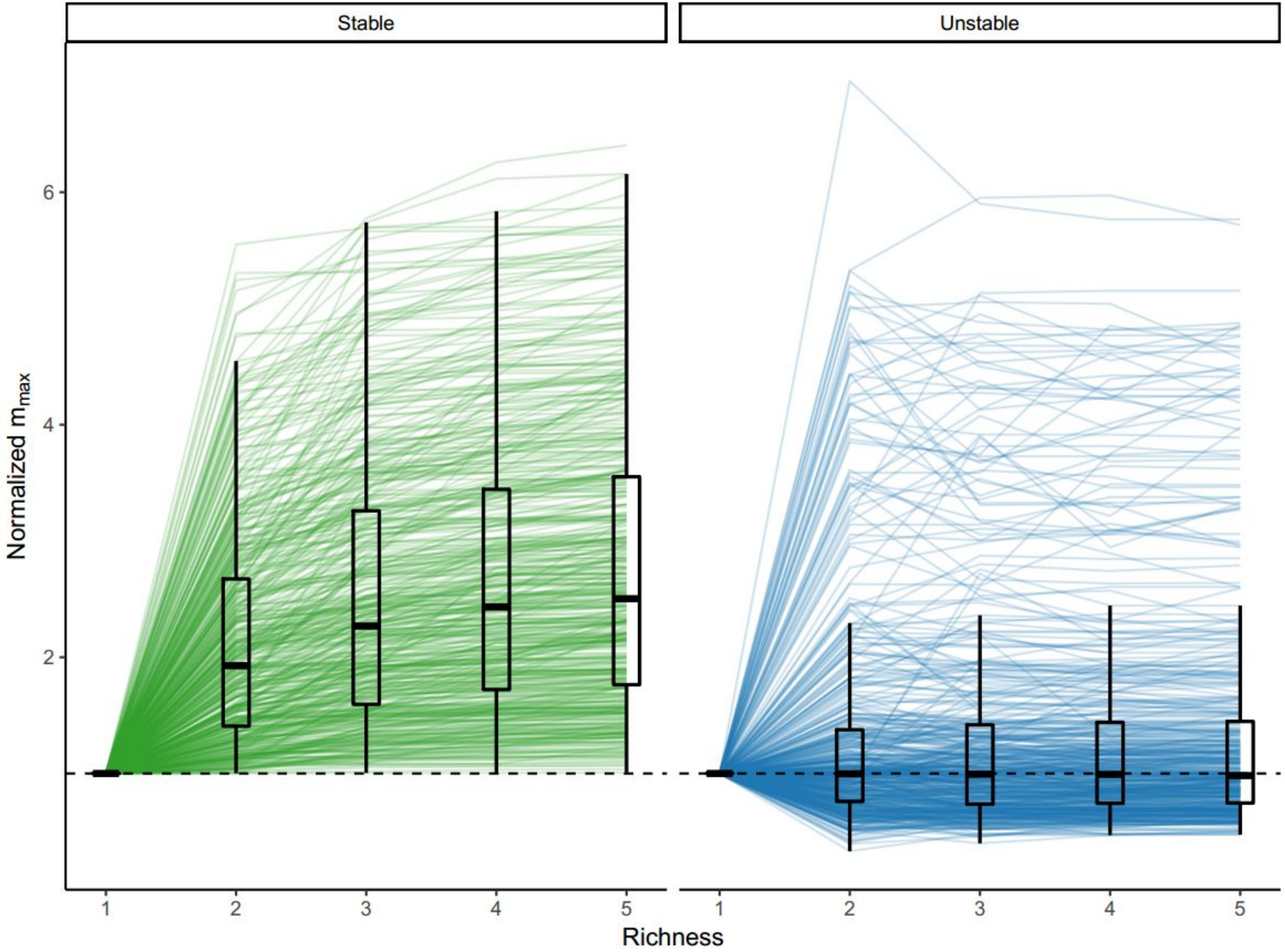
$$m < m_{max} = \beta + \frac{\alpha}{n}$$



Maximum sustainable disturbance

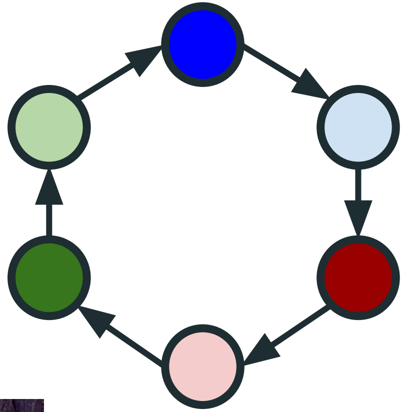


Community richness



Diversity-robustness relationship in 500 stable and 500 unstable communities

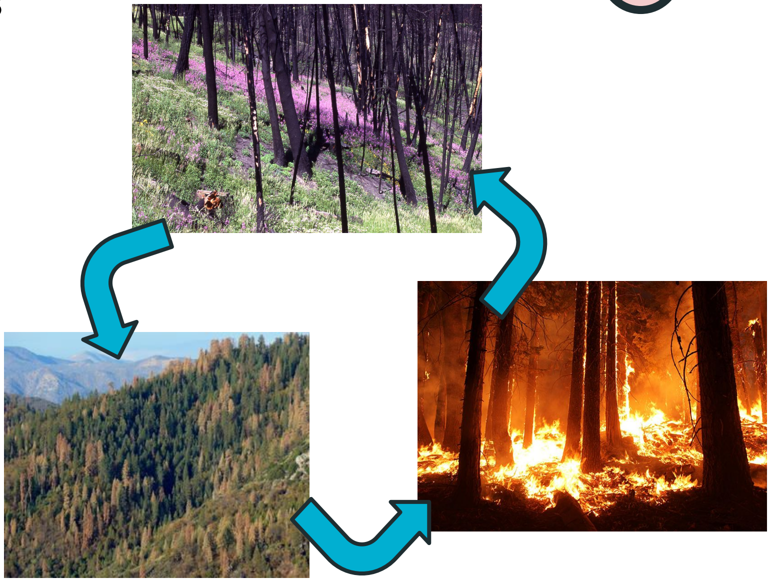
Nonsymmetric P: successional cycles



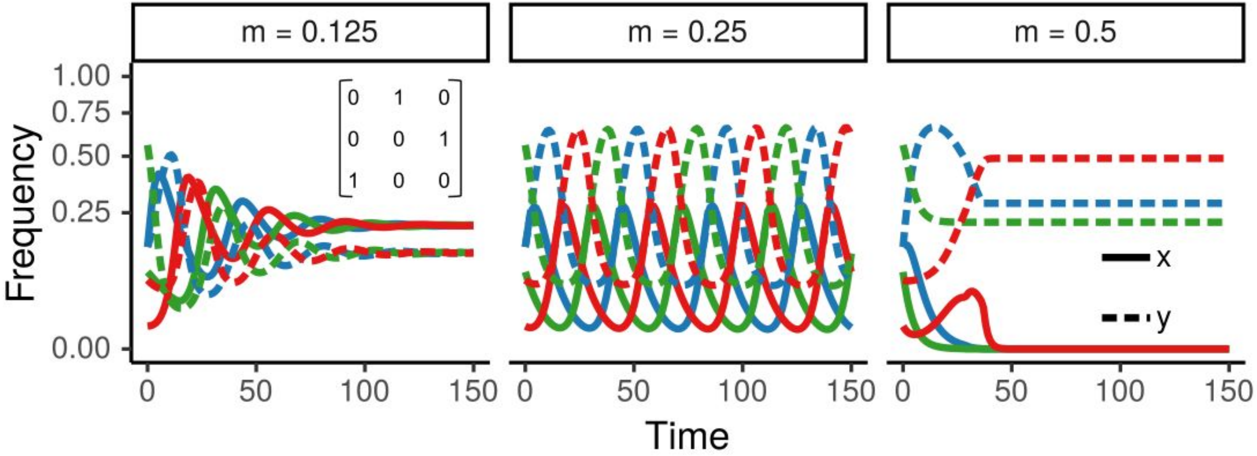
- An interesting special case is when P is a cyclic permutation matrix (e.g. rock-paper-scissors)

- A “toy” model for successional dynamics

$$P = \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \end{pmatrix}$$

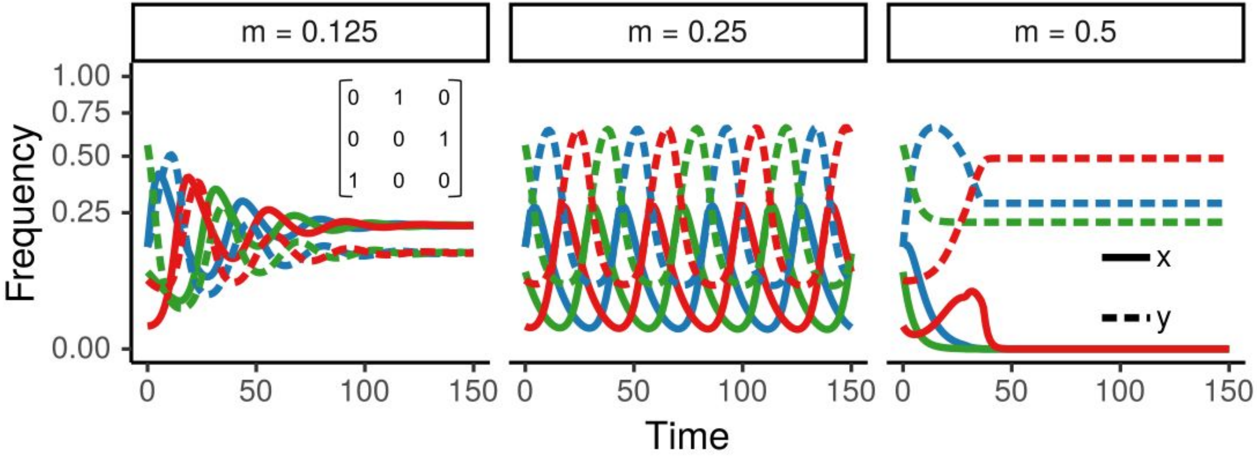


Cyclic P matrix

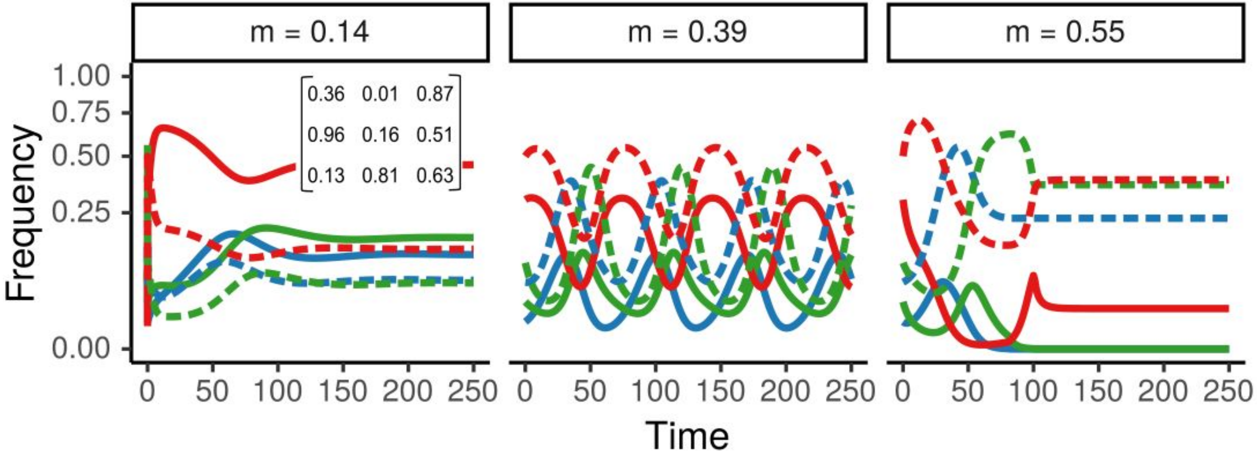


As m grows, the dynamics shift from stable equilibrium (left), to stable limit cycles (center), to instability (right)

Cyclic *P* matrix



Random nonsymmetric *P* matrix



Conclusions

- We introduce a **flexible** and **tractable** model for the dynamics of “ecosystem engineers” interacting in a landscape
- For symmetric P, the condition ***P has exactly 1 positive eigenvalue*** naturally generalizes the notion of “negative feedbacks for all species”
- Stability condition induces a **positive diversity-robustness relationship**
- For nonsymmetric P, dynamics can be much more **complex**

More details:

Metapopulations with habitat modification (bioRxiv)

bioRxiv
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Thank you!

Contact:

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