Introduction to Theoretical Ecology

What have we learned

Week 15 (Jan. 4, 2022)

Outline

1. What have we covered in this course?

2. Are analytical techniques still useful?

3. What’s out there that we did not cover?

4. General discussion

1. What have we covered in this course?

- **What is an ecological theory?**

  An explanation of a phenomenon in the form of narratives that explain how a process works or why a pattern is observed, and have become scientifically useful when expressed in a logical structure

- **What are mathematical models?**

  Transforming the idea in narrative form into testable theory involves the use of equations to describe how different aspects of a system relate to one another

  Math provides a clearer and more objective expression of relationships, it brings to light assumptions and logical errors that may be obscured in verbal hypotheses, and it places ideas and hypotheses in concise form

1. What have we covered in this course?

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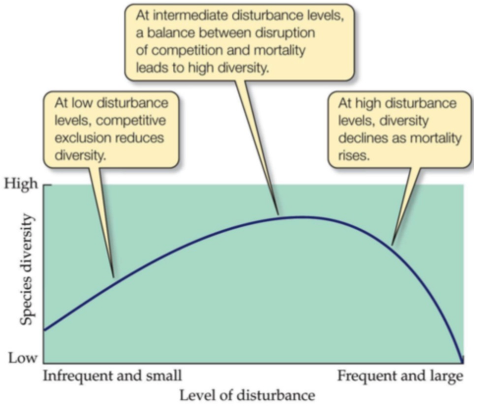
Intermediate disturbance hypothesis: fluctuations prevent competitive exclusion as no species will ever have time to exclude its competitor

Ecological phenomenon



Hypothesis / narrative

$$\frac{1}{N_i}\frac{dN_i}{dt} = a_i R - m_i(t)$$

Mathematical model

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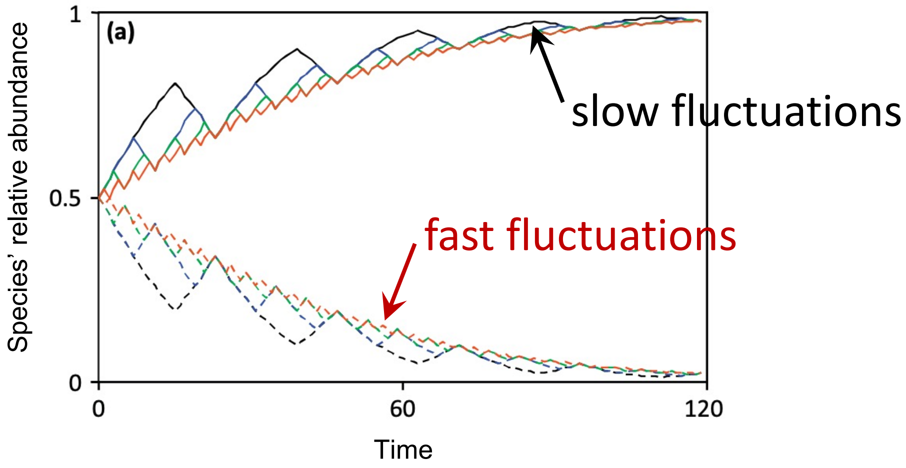
- **What is an ecological theory?**

Math provides a clearer and more objective expression of relationships, it brings to light assumptions and logical errors that may be obscured in verbal hypotheses, and it places ideas and hypotheses in concise form

Intermediate disturbance hypothesis: in a linear model, environmental fluctuation is inconsequential for competitive outcome



$$\frac{1}{N_i}\frac{dN_i}{dt} = a_i R - m_i(t)$$

Mathematical model

Fox (2013) Trends Ecol Evol

1. What have we covered in this course?

- **Classic dynamic system models in population/community ecology**

single-species population-level (Weeks 2–6)

multi-species community-level (Weeks 7–14)

Date	Lecture topic
Week 2 (05-Oct-2021)	Exponential population growth
Week 3 (12-Oct-2021)	Logistic population growth
Week 4 (19-Oct-2021)	Discrete population models
Week 5 (26-Oct-2021)	Age-structured population models
Week 6 (02-Nov-2021)	Metapopulations and patch occupancy models
Week 7 (09-Nov-2021)	Competition: graphical solution
Week 8 (16-Nov-2021)	Competition: analytical solution
Week 10 (30-Nov-2021)	Modern coexistence theory and predator-prey interactions
Week 11 (07-Dec-2021)	Predator-prey interactions
Week 12 (14-Dec-2021)	Consumer-resource dynamics
Week 13 (21-Dec-2021)	Apparent competition
Week 14 (28-Dec-2021)	Disease dynamics

1. What have we covered in this course?

- **Classic dynamic system models in population/community ecology**

	Date	Lecture topic
single-species population-level	Week 2 (05-Oct-2021)	Exponential population growth **(Integral)**
	Week 3 (12-Oct-2021)	Logistic population growth **(Local stability analysis)**
	Week 4 (19-Oct-2021)	Discrete population models
	Week 5 (26-Oct-2021)	Age-structured population models **(Eigen-analysis)**
	Week 6 (02-Nov-2021)	Metapopulations and patch occupancy models
multi-species community-level	Week 7 (09-Nov-2021)	Competition: graphical solution **(ZNGIs & vector fields)**
	Week 8 (16-Nov-2021)	Competition: analytical solution **(Invasion analysis & jacobian matrix)**
	Week 10 (30-Nov-2021)	Modern coexistence theory and predator-prey interactions
	Week 11 (07-Dec-2021)	Predator-prey interactions **(Bifurcations & cycles)**
	Week 12 (14-Dec-2021)	Consumer-resource dynamics
	Week 13 (21-Dec-2021)	Apparent competition **(Routh-Hurwitz criterion)**
	Week 14 (28-Dec-2021)	Disease dynamics

1. What have we covered in this course?

- **Common analytical techniques for dynamic systems**

Integration techniques for simple models (e.g., logistic growth)

$$\frac{dN}{dt} = rN \xrightarrow{\text{separation of variables}} N(t) = N_0 e^{rt}$$

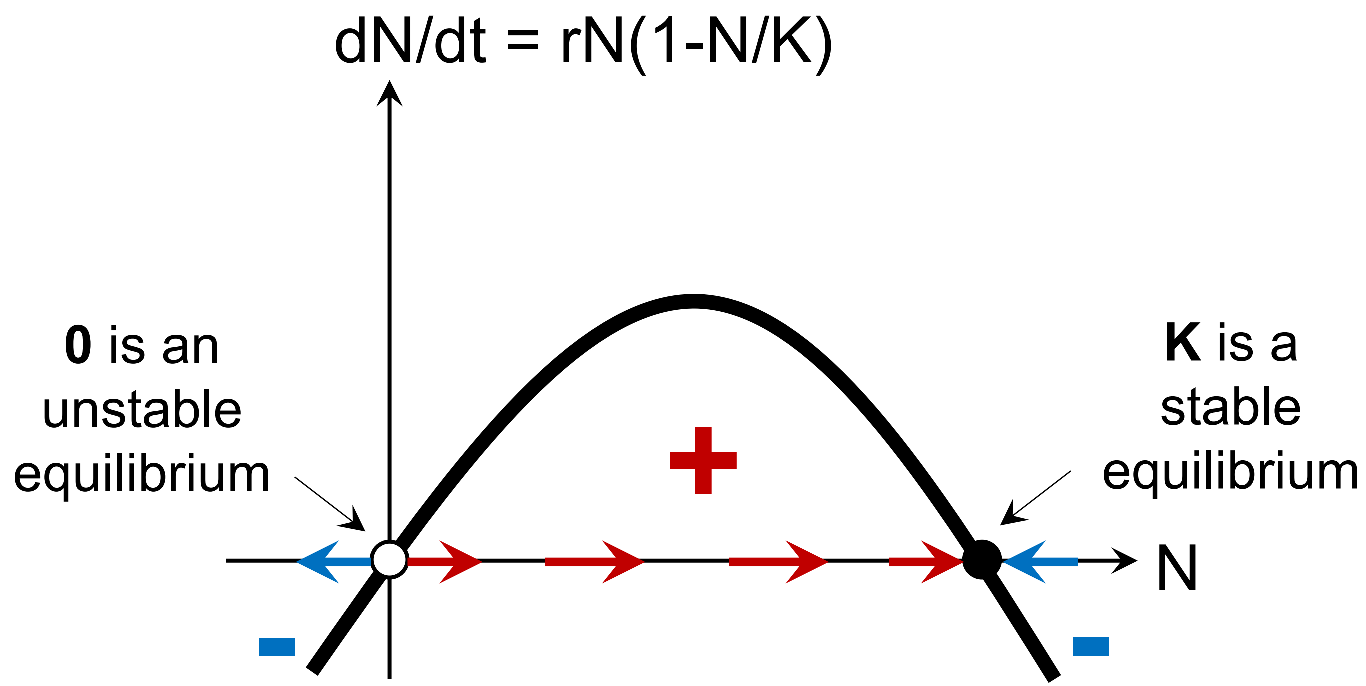
$$\frac{dN}{dt} = rN + I \xrightarrow{\text{Integral factor}} N(t) = N_0 e^{rt} + (e^{rt} - 1)\frac{I}{r}$$

$$\frac{dN}{dt} = rN\left[1 - \left(\frac{N}{K}\right)\right] \xrightarrow{\text{partial fraction decomposition}} N(t) = \frac{K}{1 - \left(\frac{N_0 - K}{N_0}\right)e^{-rt}}$$

1. What have we covered in this course?

- **Common analytical techniques for dynamic systems**

Graphical analysis of single variable model (e.g., logistic growth)



1. What have we covered in this course?

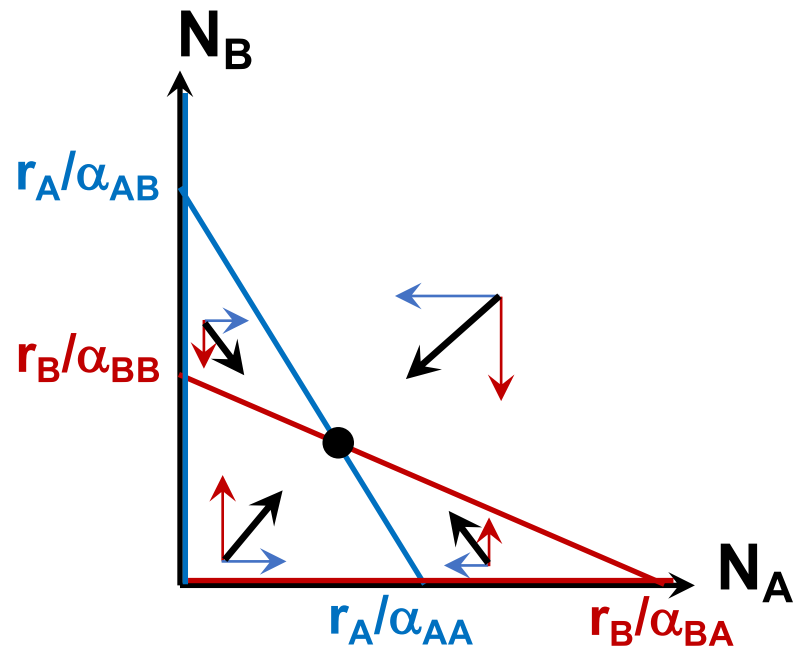
- **Common analytical techniques for dynamic systems**

State-space diagram (e.g., Lotka-Volterra models)

1. Find zero net growth isoclines (ZNGIs) that let dN/dt = 0
2. Draw ZNGIs and locate equilibrium (consider different parameter scenarios)
3. Draw vector fields and determine stability

$$\frac{dN_A}{dt} = N_A(r_A - \alpha_{AA}N_A - \alpha_{AB}N_B)$$

$$\frac{dN_B}{dt} = N_B(r_B - \alpha_{BA}N_A - \alpha_{BB}N_B)$$



1. What have we covered in this course?

- **Common analytical techniques for dynamic systems**

local stability analysis (e.g., Lotka-Volterra models)

1. Compute partial derivatives and form the jacobian matrix

$$\rightarrow J = \begin{bmatrix} (r_A - \alpha_{AA} N_A - \alpha_{AB} N_B) + N_A(-\alpha_{AA}) & N_A(-\alpha_{AB}) \\ N_B(-\alpha_{BA}) & (r_B - \alpha_{BA} N_A - \alpha_{BB} N_B) + N_B(-\alpha_{BB}) \end{bmatrix}$$

2. Evaluate the jacobian matrix at the equilibrium

$$\rightarrow J = \begin{bmatrix} -\alpha_{AA} N_A^* & -\alpha_{AB} N_A^* \\ -\alpha_{BA} N_B^* & -\alpha_{BB} N_B^* \end{bmatrix}$$

3. Check conditions under which eigenvalues have negative real parts

$$\rightarrow N_A^*, N_B^* > 0 \ \& \ \alpha_{AA}\alpha_{BB} > \alpha_{BA}\alpha_{AB}$$

1. What have we covered in this course?

- **Common analytical techniques for dynamic systems**

<u>Invasion analysis (e.g., Lotka-Volterra models)</u>

1. Compute monoculture equilibrium by dropping one species (e.g., only N_A)

$$\rightarrow E_A = \frac{r_A}{\alpha_{AA}}$$

2. Evaluate invasion growth rate (IGR; per capita growth rate when rare)

$$\rightarrow IGR_B = r_B - \alpha_{BA} \times \left(\frac{r_A}{\alpha_{AA}} \right) - \alpha_{BB} \times 0$$

3. Check conditions under which invasion is possible

$$\rightarrow \frac{\alpha_{AA}}{r_A} > \frac{\alpha_{BA}}{r_B}$$

1. What have we covered in this course?

- **Common analytical techniques for dynamic systems**

<u>Timescale separation (e.g., MacArthur consumer-resource model)</u>

1. Assume fast variable reaches quasi-equilibrium while slow variable remains constant
2. Substitute fast variables' quasi-equilibrium into the the slow variable equation

$$\frac{dR_1}{dt} = R_1\left[r_1\left(1 - \frac{R_1}{K_1}\right) - a_{1A}N_A - a_{1B}N_B\right]$$

$$\frac{dR_2}{dt} = R_2\left[r_2\left(1 - \frac{R_2}{K_2}\right) - a_{2A}N_A - a_{2B}N_B\right]$$

$$\frac{dN_A}{dt} = N_A\left[ea_{1A}R_1 + ea_{2A}R_2 - m_A\right]$$

$$\frac{dN_B}{dt} = N_B\left[ea_{1B}R_1 + ea_{2B}R_2 - m_B\right]$$

$$\widehat{R_1} = \frac{K_1}{r_1}\left[r_1 - a_{1A}N_A - a_{1B}N_B\right]$$

$$\widehat{R_2} = \frac{K_2}{r_2}\left[r_2 - a_{2A}N_A - a_{2B}N_B\right]$$

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Quasi-equilibrium of resource 1

Quasi-equilibrium of resource 2

$$\frac{dN_A}{dt} = N_A\left[ea_{1A}\left(K_1 - \frac{K_1}{r_1}a_{1A}N_A - \frac{K_1}{r_1}a_{1B}N_B\right) + ea_{2A}\left(K_2 - \frac{K_2}{r_2}a_{2A}N_A - \frac{K_2}{r_2}a_{2B}N_B\right) - m_A\right]$$

$$= N_A\left[\left(ea_{1A}K_1 + ea_{2A}K_2 - m_A\right) - \left(\frac{eK_1}{r_1}a_{1A}^2 + \frac{eK_2}{r_2}a_{2A}^2\right)N_A - \left(\frac{eK_1}{r_1}a_{1A}a_{1B} + \frac{eK_2}{r_2}a_{2A}a_{2B}\right)N_B\right]$$

Intrinsic growth rate of species A

Intraspecific competition on species A

Interspecific competition on species A

1. What have we covered in this course?

- **Work flow to create a model**

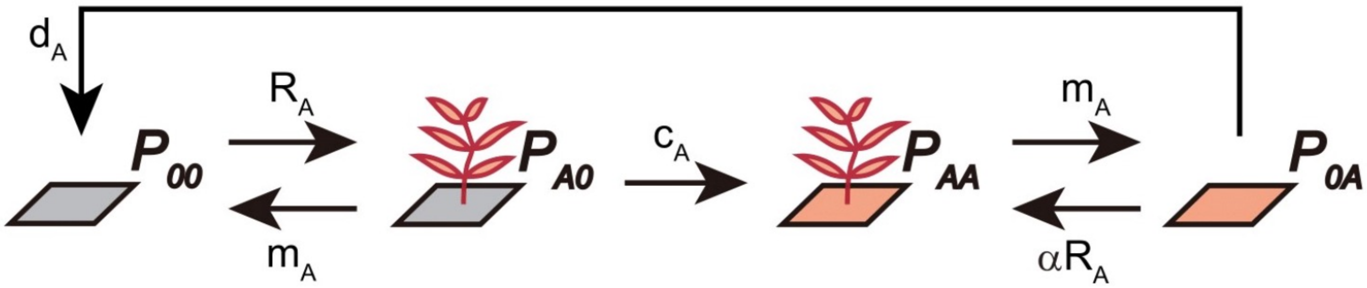
  Step 1: Formulate the motivating question

  Step 2: Determine the basic ingredients

  Step 3: Qualitatively describe the biological system

  Step 4: Quantitatively describe the biological system

  Step 5: Analyze the model



1. What have we covered in this course?

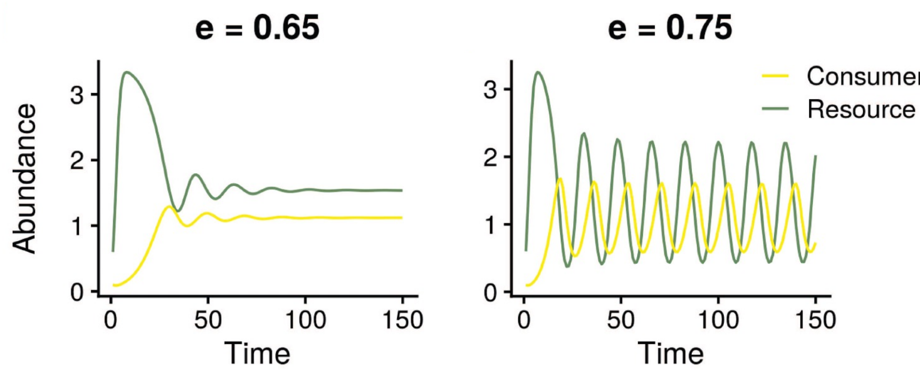
- **Common figures in theoretical ecology papers**

Rosenzweig-MacArthur model

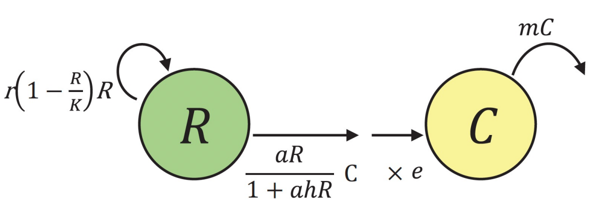
$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \left(\frac{aR}{1 + ahR}\right)C$$

$$\frac{dC}{dt} = e\left(\frac{aR}{1 + ahR}\right)C - mC$$

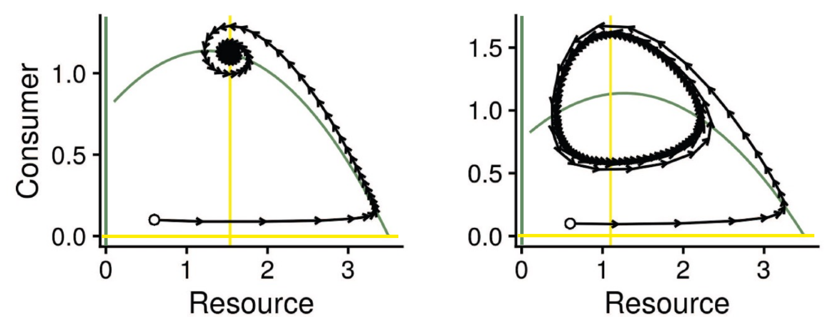
Time series plots



Stock-and-flow model diagram



State-space diagram (ZNGIs)



Grainger et al (2022) Am Nat

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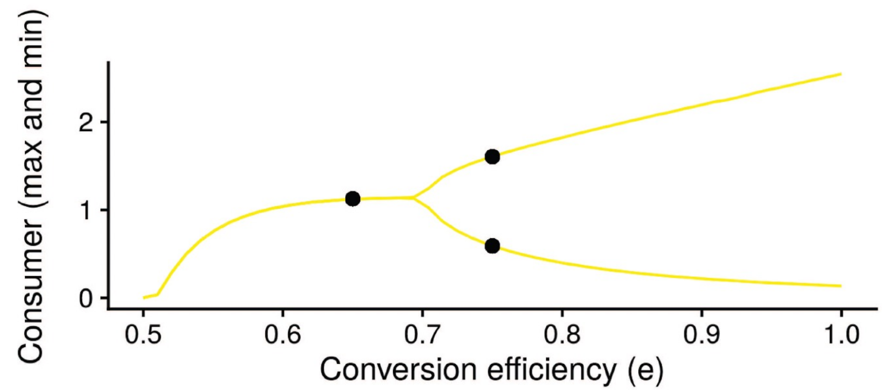
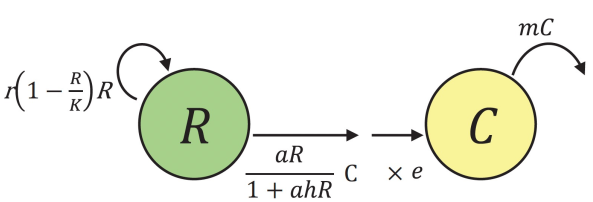
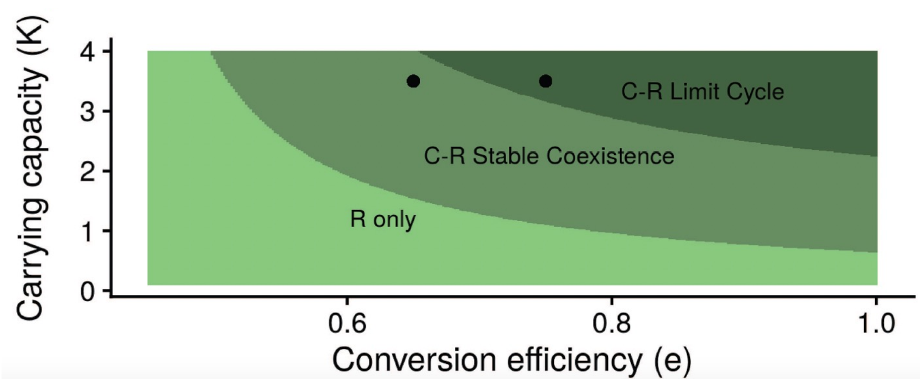
One dimension bifurcation diagram



Stock-and-flow model diagram



Two dimension parameter space



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1. What have we covered in this course?

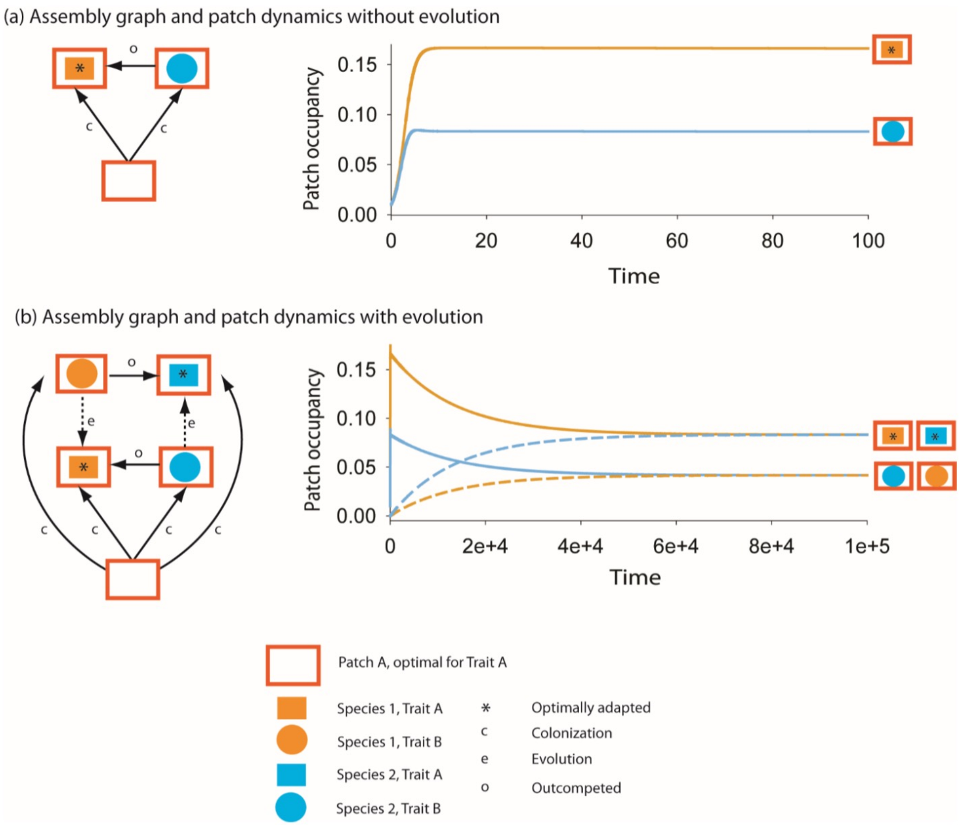
- **Simulation platform for dynamic systems**

```
### (1) Model specigication
LV_competition_model <- function(Time, State, Pars){
      with(as.list(c(State, Pars)), {
         dN1 = N1 * (r1 - a11 * N1 - a12 * N2)
         dN2 = N2 * (r2 - a21 * N1 - a22 * N2)
         return(list(c(dN1, dN2)))
      })
 }

### (2) Parameter setup
times <- seq(0, 100, by = 0.1)
state <- c(N1 = 10, N2 = 10)
parms <- c(r1 = 1.4, r2 = 1.2, a11 = 1/200, a21 = 1/400, a22 = 1/200, a12 = 1/300)

### (3) Run the ode solver
pop_size <- ode(func=LV_competition_model, times=times, y=initial, parms=parms)
```

2. Are analytical techniques still useful?

- **Theoretical papers are often a combination of simulations and analytical treatments**

Patch occupancy model with evolution: local evolutionary priority effects result in regional neutrality (species have similar trait distributions and relative abundances)



Leibold et al. (2018) PNAS

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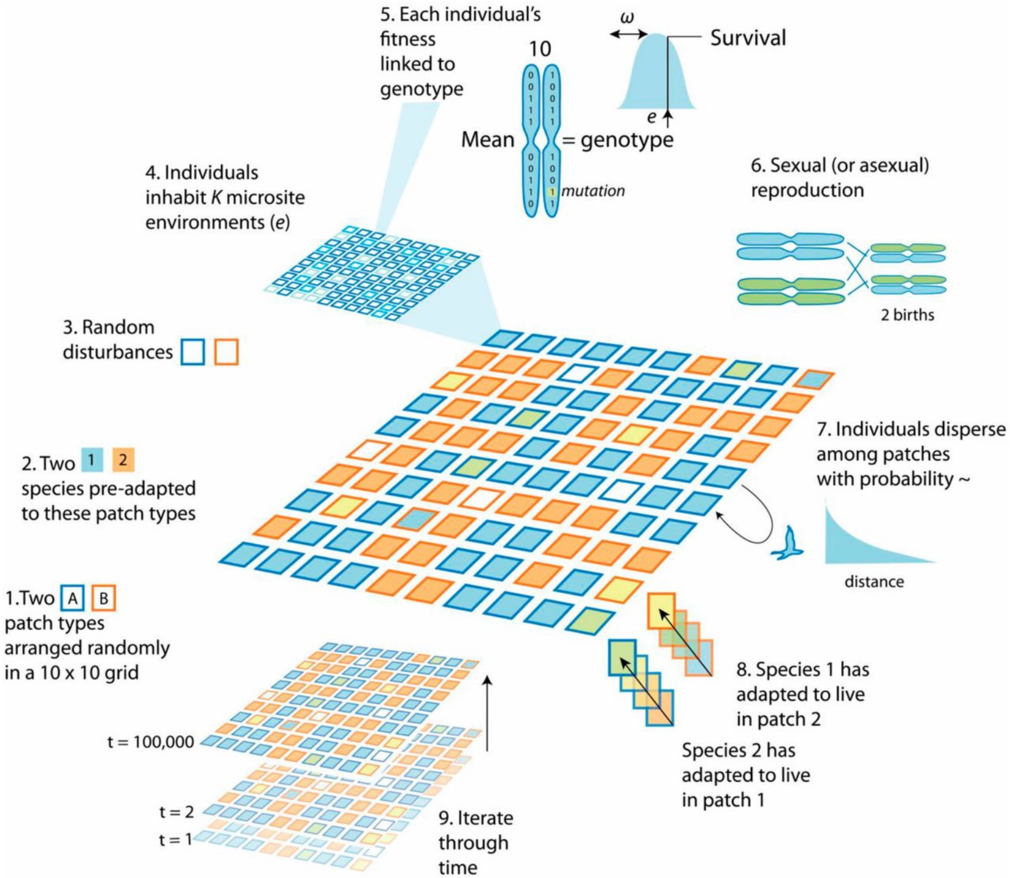

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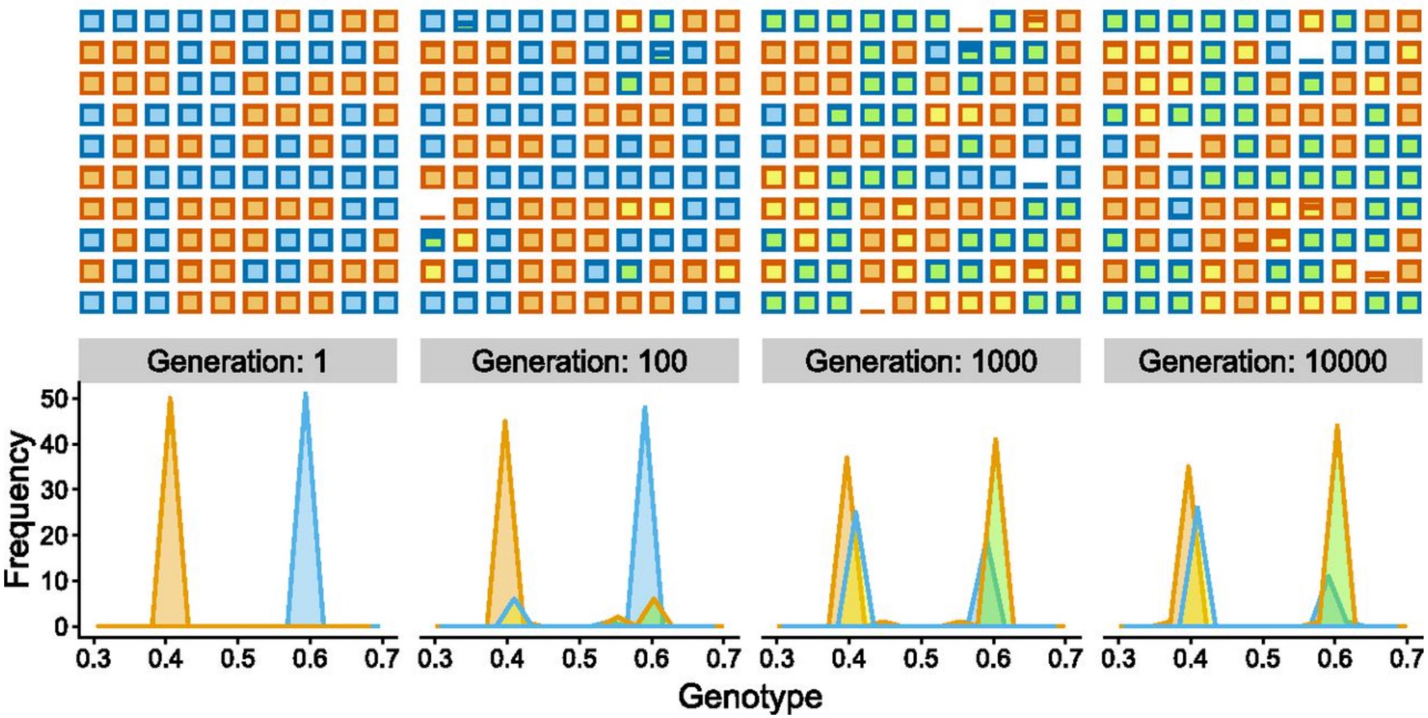

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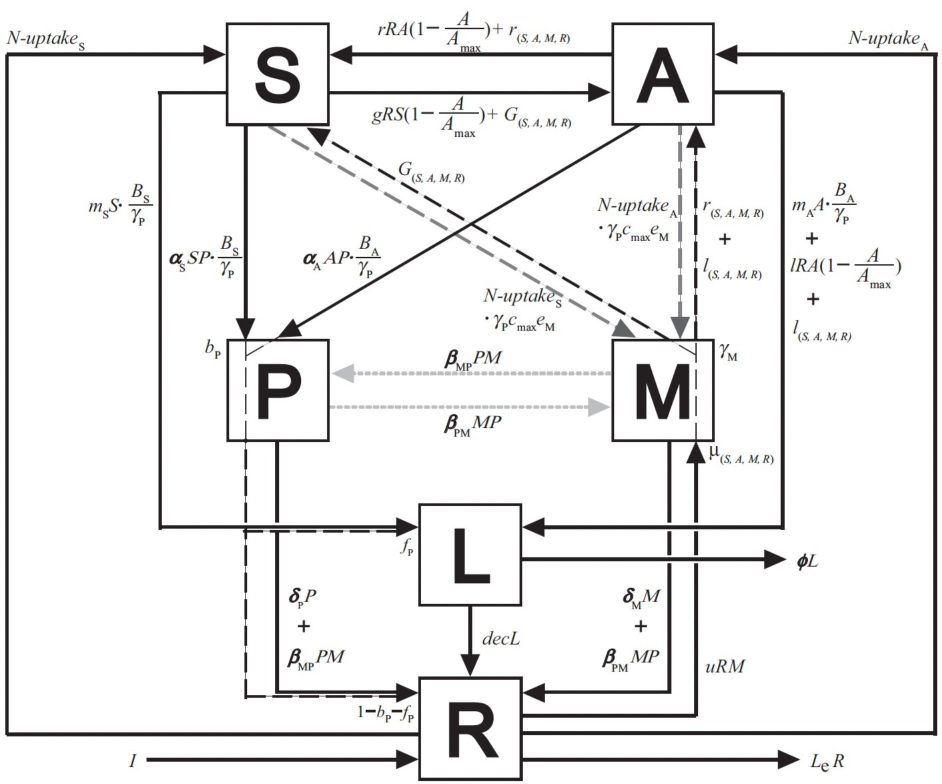
Trait-based plant-soil feedback model: What traits determine the strength of plant-soil feedback and how does it vary with soil microbial community composition?



Ke et al. (2015) New Phyt

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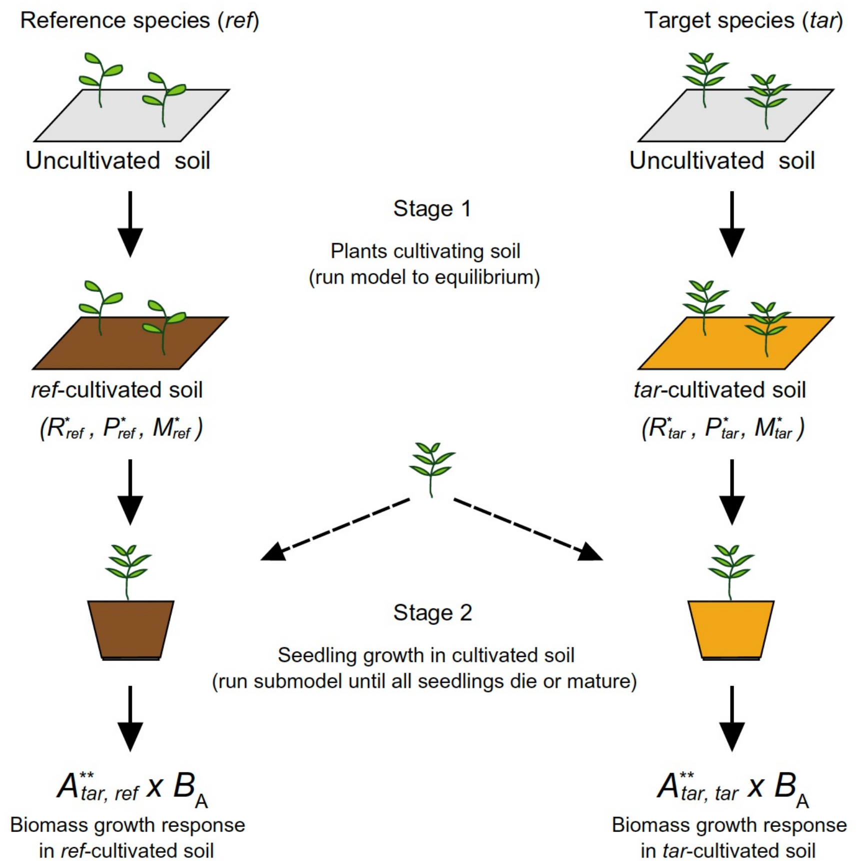
Trait-based plant-soil feedback model: Simulation experiment to see what traits determine the strength of plant-soil feedback



Ke et al. (2015) New Phyt

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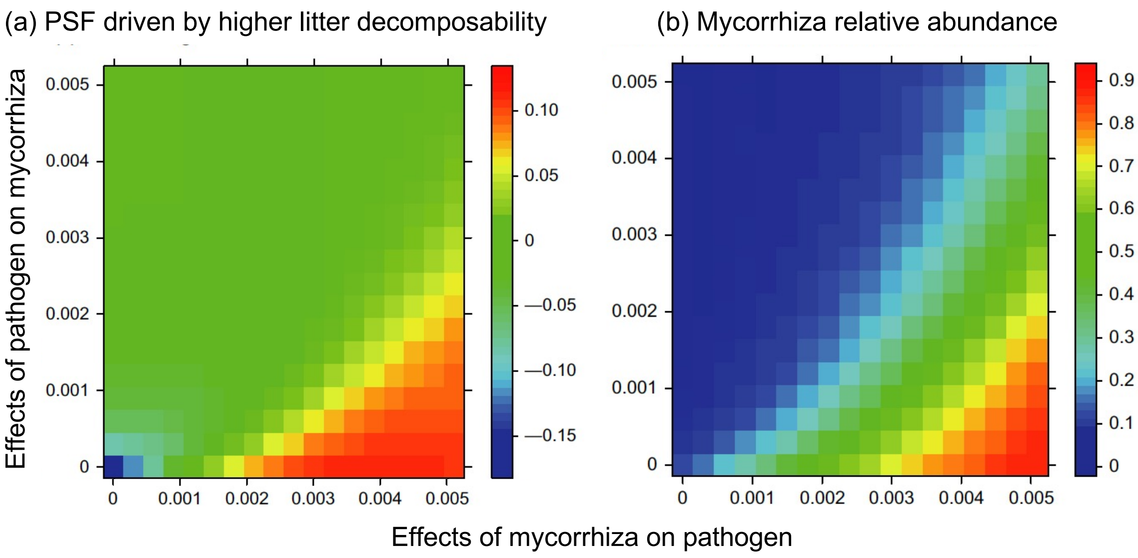
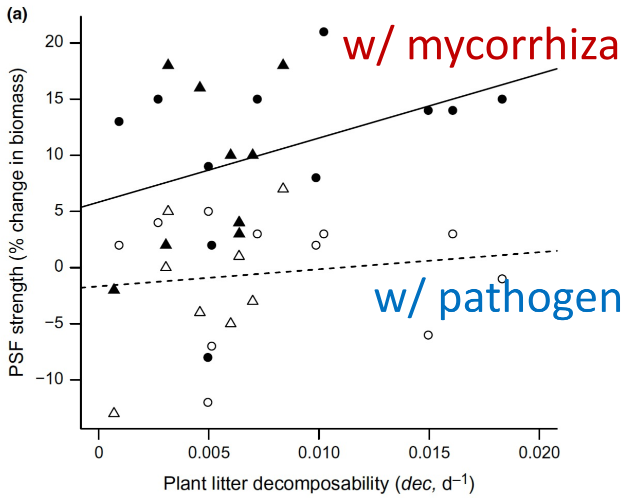
Trait-based plant-soil feedback model: litter decomposibility is an important trait determining plant-soil feedback when mycorrhizal fungi are dominant in the soil





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Trait-based plant-soil feedback model: analytical analysis of the microbe free equilibrium was useful when picking model parameters

Microbe free equilibrium

$$A^*_{MF} = \frac{A_{\max}}{-2a'} \cdot \left[a' - c' + \sqrt{(a' - c')^2 - d'} \right],$$

$$S^*_{MF} = \eta \times A^*_{MF},$$

$$R^*_{MF} = \frac{IA_{\max} + \left(\frac{dec}{dec+\phi}\right) \cdot (m_S n_S \eta + m_A n_A) A_{\max} A^*_{MF}}{L_e A_{\max} + A^*_{MF}(A_{\max} - A^*_{MF}) \cdot \left[r n_S + g\eta(n_A - n_S) + l\left(\frac{\phi}{dec+\phi}\right)\right]},$$

$$L^*_{MF} = \left[m_S n_S \eta + m_A n_A + l R^*_{MF}\left(1 - \frac{A^*_{MF}}{A_{\max}}\right)\right] \cdot \left(\frac{A^*_{MF}}{dec+\phi}\right).$$

Feasibility

$$\frac{I}{L_e} > \frac{m_A}{g\eta}$$

Invasion criterion for pathogens

$$\frac{1}{\alpha_S \eta n_S + \alpha_A n_A} \cdot \frac{\delta_P}{b_P} < A^*_{MF}.$$

Invasion criterion for mycorrhiza

$$\frac{\delta_M}{(1 - n_{\min}) \cdot u} > R^*_{MF}.$$

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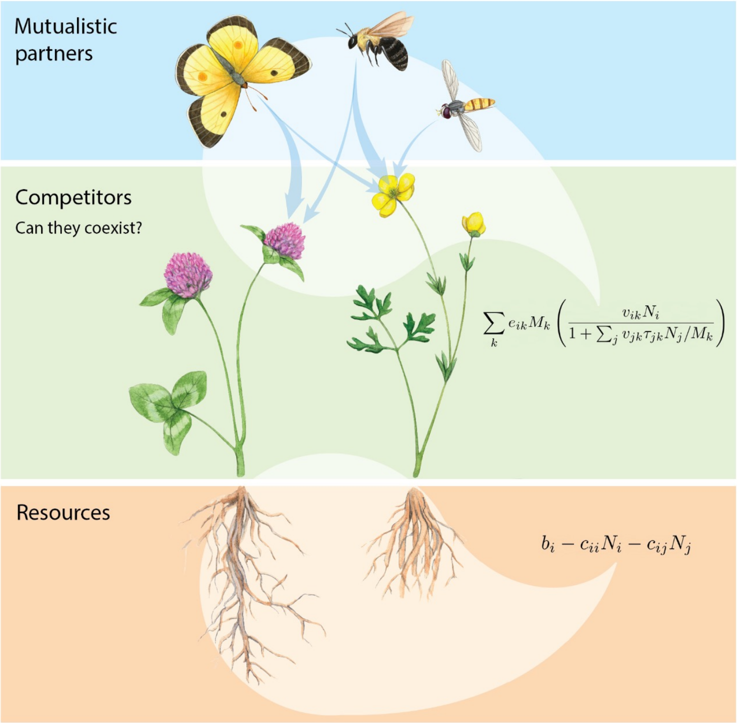
Competition for mutualism partners: incorporate competition for mutualism partners into plant-plant interaction and modern coexistence theory



$$\frac{dN_i}{dt} = N_i(b_i - c_{ii}N_i - c_{ij}N_j) + \sum_k e_{ik} M_k \left(\frac{v_{ik} N_i}{1 + \sum_j v_{jk} \tau_{jk} N_j / M_k} \right),$$

$$\frac{dM_k}{dt} = M_k(\beta_k - \delta_k M_k) + \sum_i \frac{\mu_{ik} M_k}{1 + \sigma_{ik} M_k} \left(\frac{v_{ik} N_i}{1 + \sum_j v_{jk} \tau_{jk} N_j / M_k} \right).$$

Johnson (2021) Ecology

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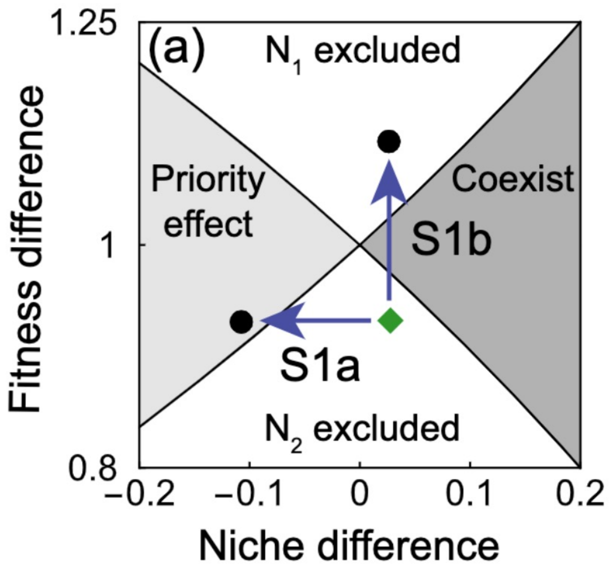
Competition for mutualism partners: incorporate competition for mutualism partners into plant-plant interaction and modern coexistence theory

Timescale separation

$$\alpha_{ij} = \frac{1}{r_i}\left(\overbrace{c_{ij}}^{\text{Resource competition}} + \overbrace{\sum_k e_{ik} v_{ik} v_{jk} \tau_{jk}}^{\text{Competition for commodities}} - \overbrace{\sum_k \frac{e_{ik} v_{ik} v_{jk} \mu_{jk}}{\delta_k}}^{\text{Indirect effects mediated by mutualistic partners}} \right)$$

$$r_i = \overbrace{b_i}^{\text{Per capita population growth rate on resources}} + \overbrace{\sum_k \frac{e_{ik} v_{ik} \beta_k}{\delta_k}}^{\text{Per capita population growth rate on commodities}}$$

$$\rho = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{22}\alpha_{11}}} \qquad \frac{\kappa_2}{\kappa_1} = \sqrt{\frac{\alpha_{12}\alpha_{11}}{\alpha_{21}\alpha_{22}}}.$$



Johnson (2021) Ecology

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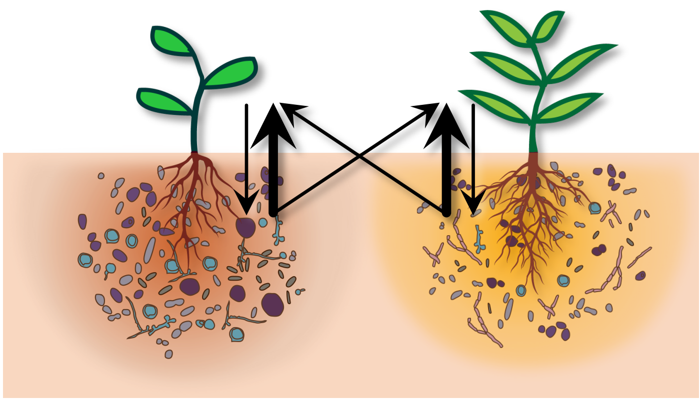
Demographic plant-soil feedback model: Will plant competitive outcome depend on (1) which demographic rate is affected by microbes and (2) the decay rates of soil microbes



microbes change instantaneously following plant colonization/death

$$\frac{dN_i}{dt}\frac{1}{N_i} = r_i\left(1 - c_{ii}N_i - c_{ij}N_j + \sigma_{ii}S_i^* + \sigma_{ij}S_j^*\right)$$

single parameter representing plant population growth

microbial effect on plant per capita growth rate

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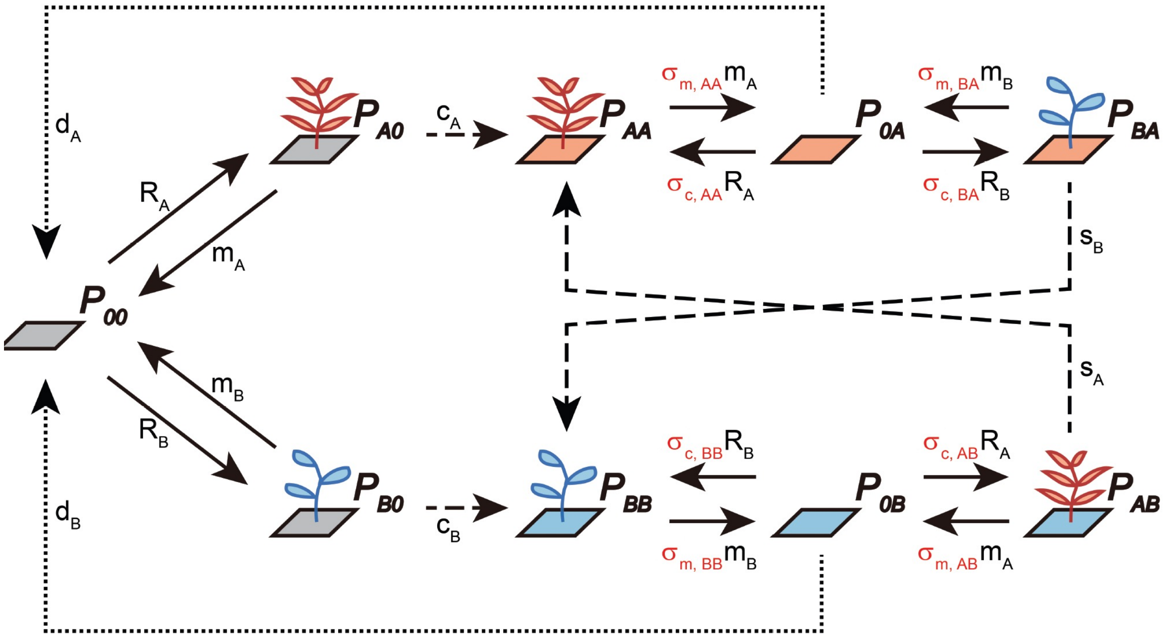
Demographic plant-soil feedback model: Patch occupancy model incorporating (1) the demographic context of microbial effect and (2) the dynamic rates of soil microbes



* $R_A = r_A(\boldsymbol{P_{A0}} + \sigma_{f,AA}\boldsymbol{P_{AA}} + \sigma_{f,AB}\boldsymbol{P_{AB}})$; $R_B = r_B(\boldsymbol{P_{B0}} + \sigma_{f,BA}\boldsymbol{P_{BA}} + \sigma_{f,BB}\boldsymbol{P_{BB}})$

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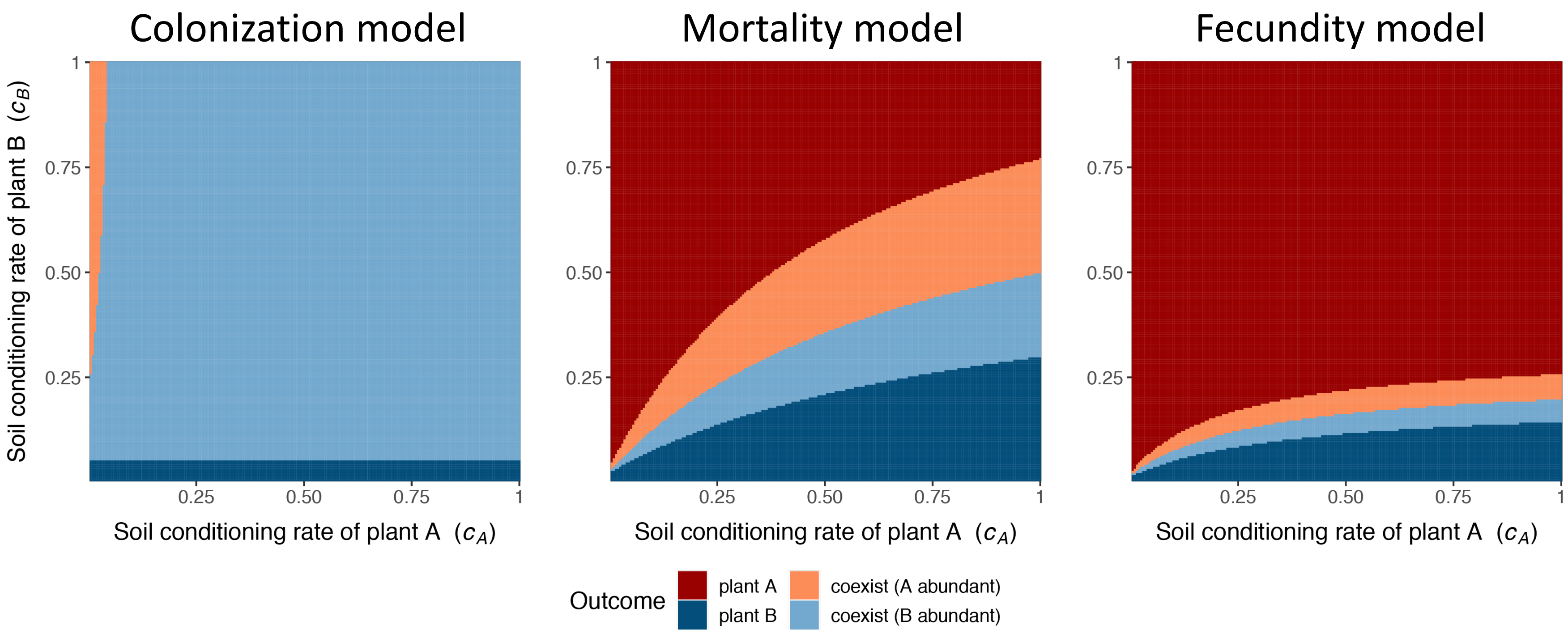
Demographic plant-soil feedback model: Microbes affect competitive hierarchy in the mortality and fecundity model, but promote coexistence in the colonization model



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2. Are analytical techniques still useful?

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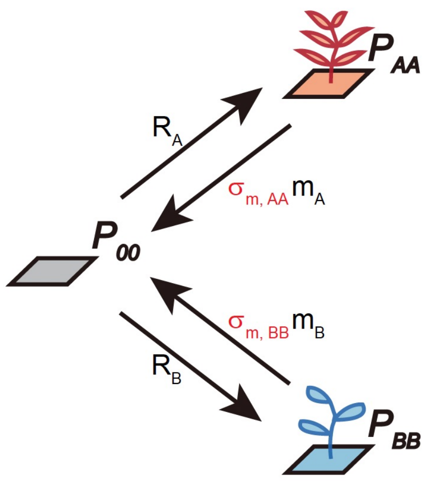
Demographic plant-soil feedback model: simplified models with different assumptions about the dynamic rates reveal the underlying mechanism for coexistence

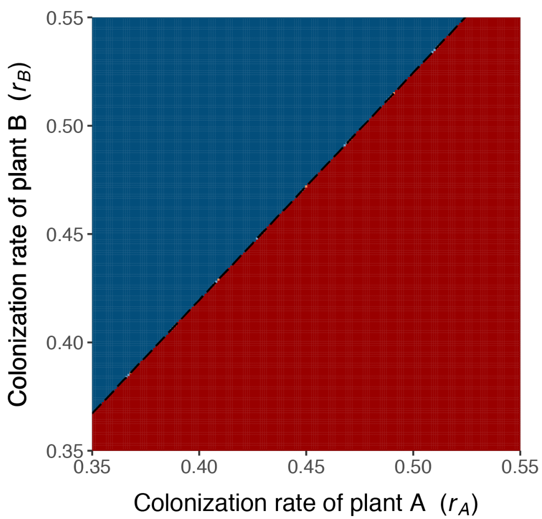
Fast conditioning + fast decay



* $R_A = r_A(\sigma_{f,AA} P_{AA})$; $R_B = r_B(\sigma_{f,BB} P_{BB})$

mutual invasion is not possible

$$\frac{r_B \sigma_{f,BB}}{m_B \sigma_{m,BB}} \text{ vs. } \frac{r_A \sigma_{f,AA}}{m_A \sigma_{m,AA}}$$



Ke and Levine (2021) Am Nat

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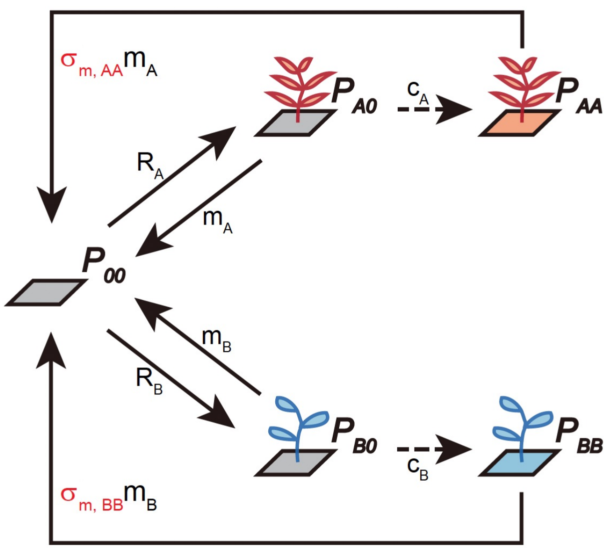
Demographic plant-soil feedback model: simplified models with different assumptions about the dynamic rates reveal the underlying mechanism for coexistence

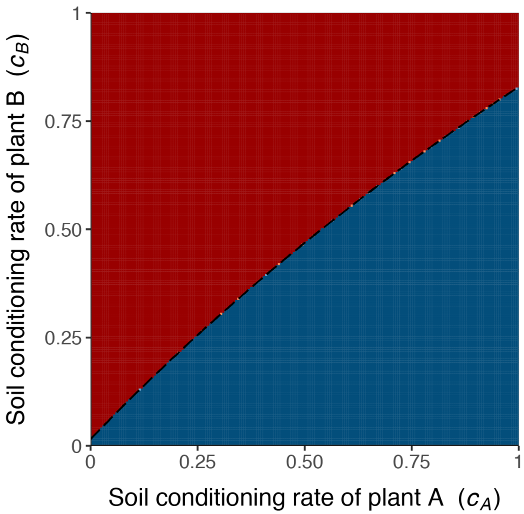
Slow conditioning + fast decay



* $R_A = r_A(P_{A0} + \sigma_{f,AA} P_{AA})$; $R_B = r_B(P_{B0} + \sigma_{f,BB} P_{BB})$

mutual invasion is not possible

$$\frac{c_B r_B \sigma_{f,BB} + r_B m_B \sigma_{m,BB}}{c_B m_B \sigma_{m,BB} + m_B^2 \sigma_{m,BB}} \quad \text{vs.} \quad \frac{c_A r_A \sigma_{f,AA} + r_A m_A \sigma_{m,AA}}{c_A m_A \sigma_{m,AA} + m_A^2 \sigma_{m,AA}}$$



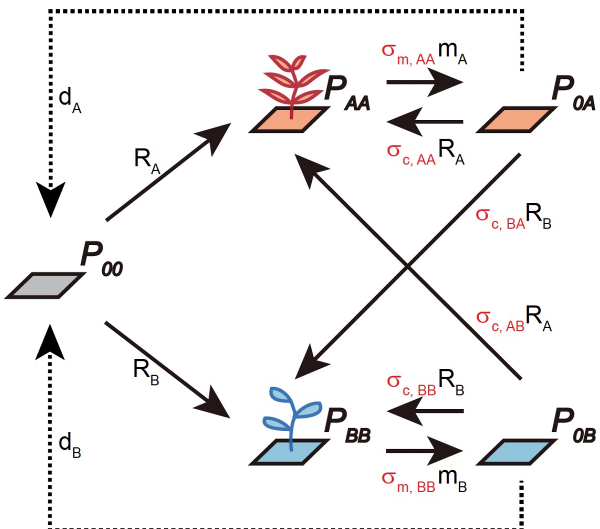
Ke and Levine (2021) Am Nat

2. Are analytical techniques still useful?

- **Theoretical papers are often a combination of simulations and analytical treatments**

Demographic plant-soil feedback model: coexistence occurs only when microbial effects are cross-generational, either by affecting colonization or if they decay slowly

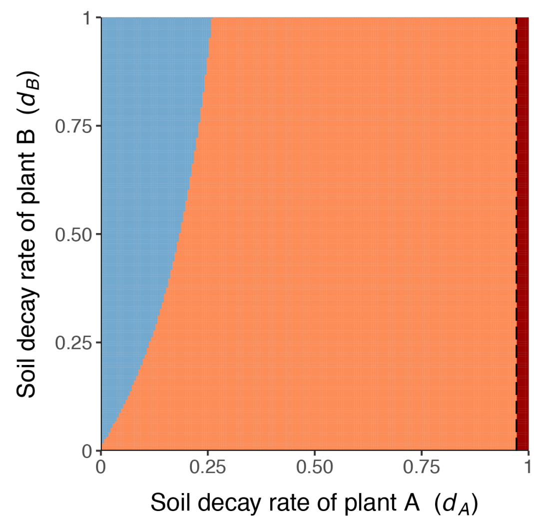
Fast conditioning + slow decay



* $R_A = r_A(\sigma_{f,AA} P_{AA})$; $R_B = r_B(\sigma_{f,BB} P_{BB})$

mutual invasion is possible, e.g., when:

$$d_A < \frac{r_A\sigma_{f,AA}\left(r_B\sigma_{f,BB} - m_B\sigma_{m,BB}\right)\left(r_A\sigma_{f,AA}m_B\sigma_{m,BB}\sigma_{c,AA} - r_B\sigma_{f,BB}m_A\sigma_{m,AA}\right)}{r_B\sigma_{f,BB}\left(r_B\sigma_{f,BB}m_A\sigma_{m,AA} - r_A\sigma_{f,AA}m_B\sigma_{m,BB}\right)}$$

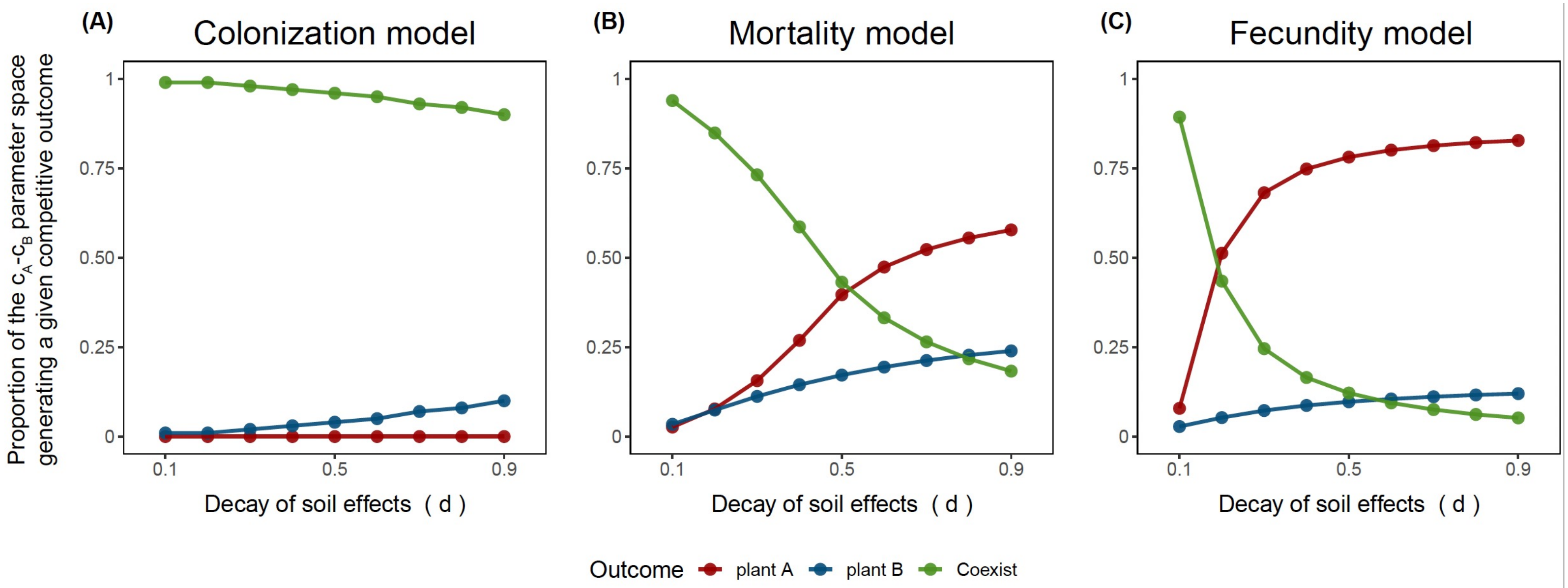


Ke and Levine (2021) Am Nat

2. Are analytical techniques still useful?

- **Theoretical papers are often a combination of simulations and analytical treatments**

Demographic plant-soil feedback model: coexistence occurs when microbial effects decay slowly (analytical prediction confirmed by simulations)

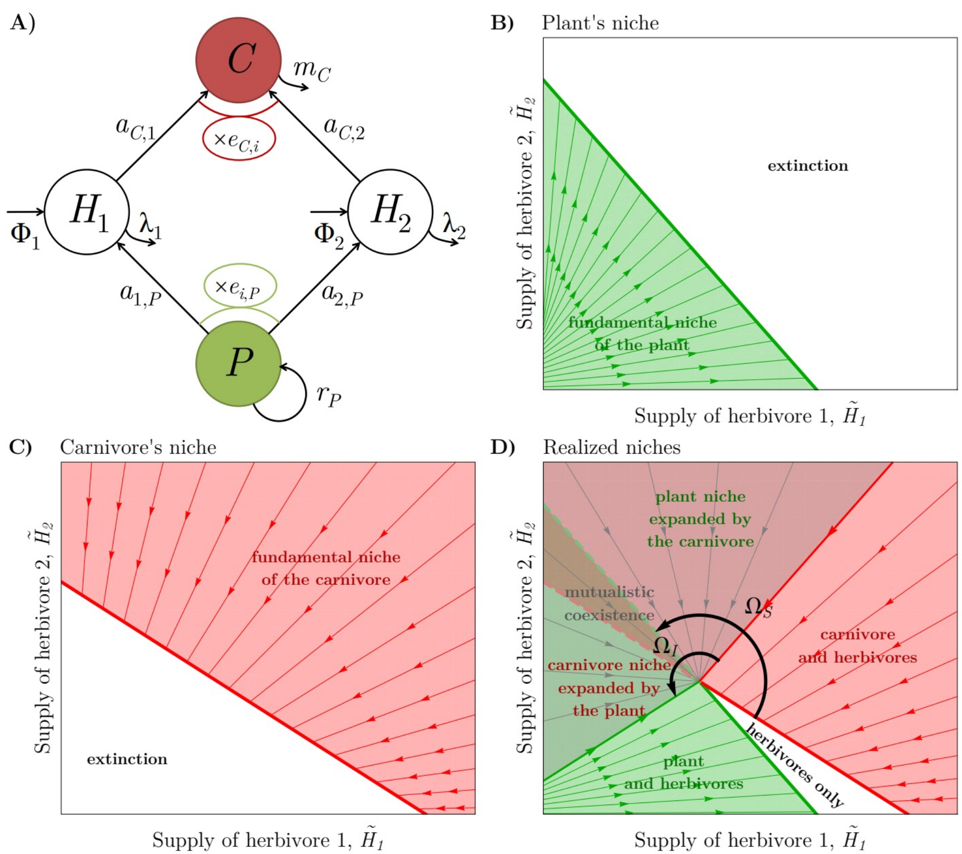


Ke and Levine (2021) Am Nat

2. Are analytical techniques still useful?

- **Theoretical papers are often a combination of simulations and analytical treatments**

Niche theory: extensions of Tilman's graphical approach to other limiting factors

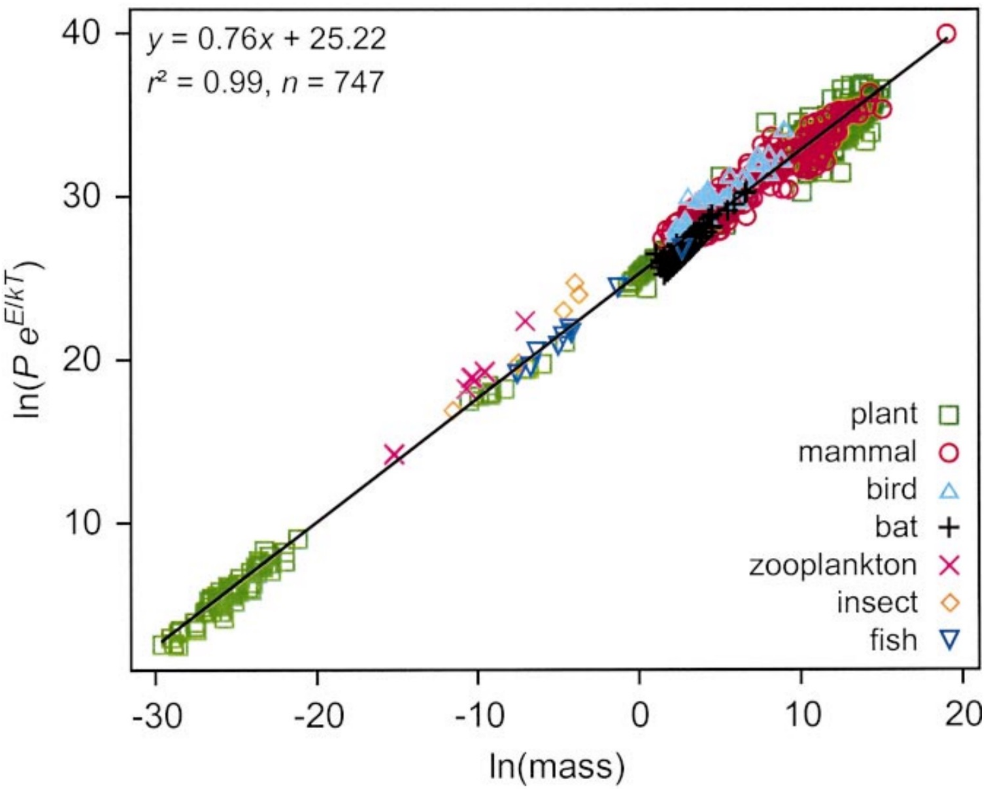


Koffel et al (2021) Ecol Monogr

3. What's out there that we did not cover?

- **Many!**

Ecological theories that are not related to dynamic systems (e.g., metabolic theory)



Brown (2004) Ecology

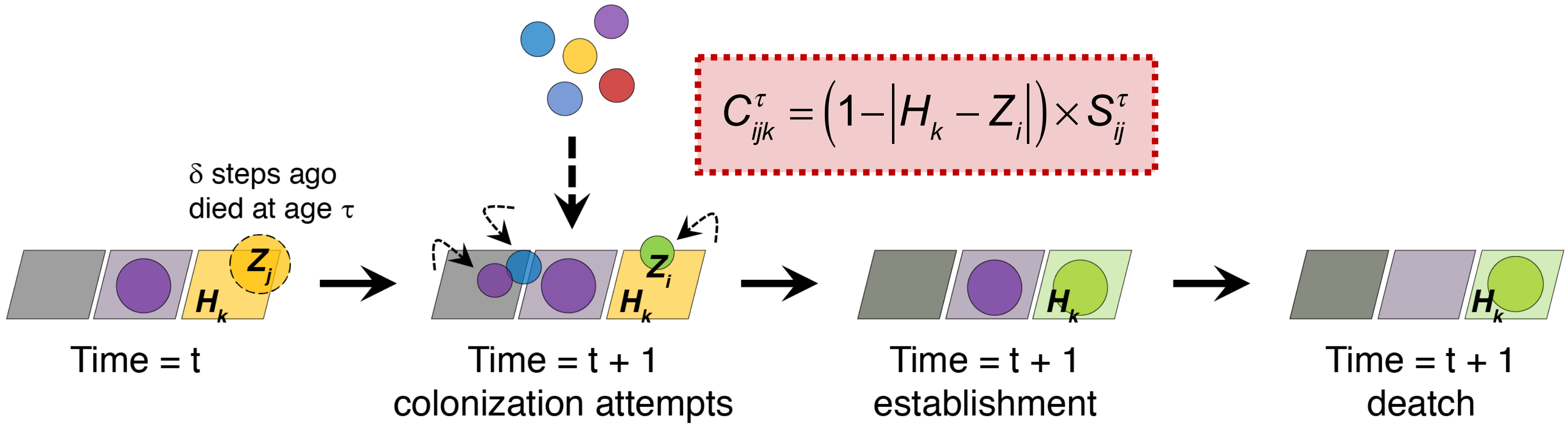
3. What's out there that we did not cover?

- **Many!**

Complicated models that rely on computer simulations (i.e., individual-based models)

IBM to study how microbial legacies affect plant community assembly
Traits: plant trait (Z_i), habitat quality (H_k), microbial legacy effect (S_{ij})
Processes: dispersal, competition for recruitment, establishment, death

$$C_{ijk}^{\tau} = \left(1 - \left|H_k - Z_i\right|\right) \times S_{ij}^{\tau}$$



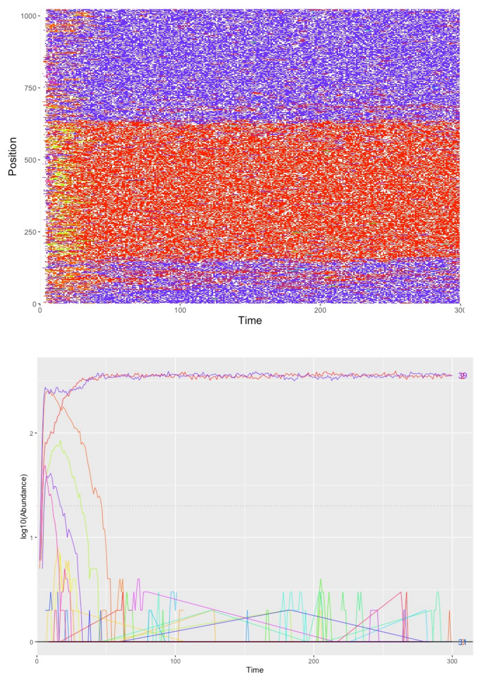
Ke et al (2021) New Phyt

3. What's out there that we did not cover?

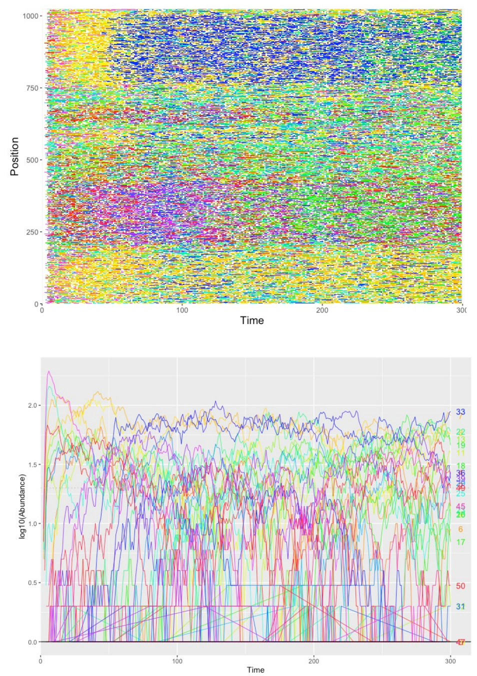
- **Many!**

Complicated models that rely on computer simulations (i.e., individual-based models)

Positive microbial legacies
promote dominance of few species



Negative microbial legacies
promote diversity and turnover



Ke et al (2021) New Phyt

4. General discussion

- **Continuous feedback between empirical work and model**