Incorporating community assembly into Modern Coexistence Theory

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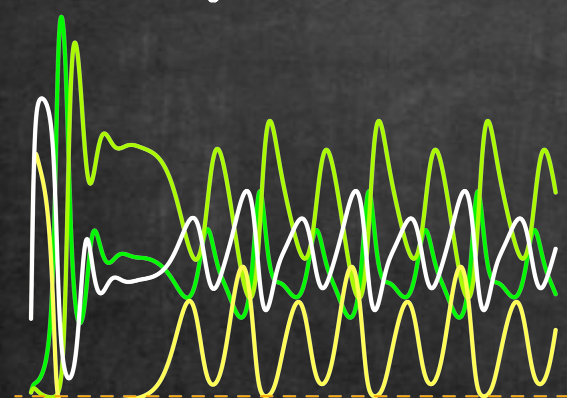
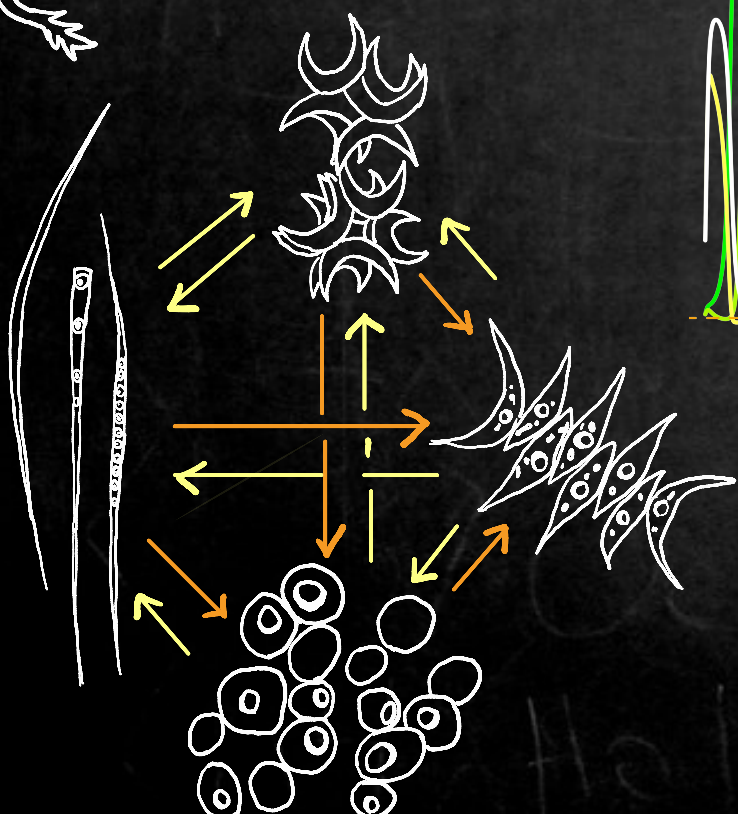
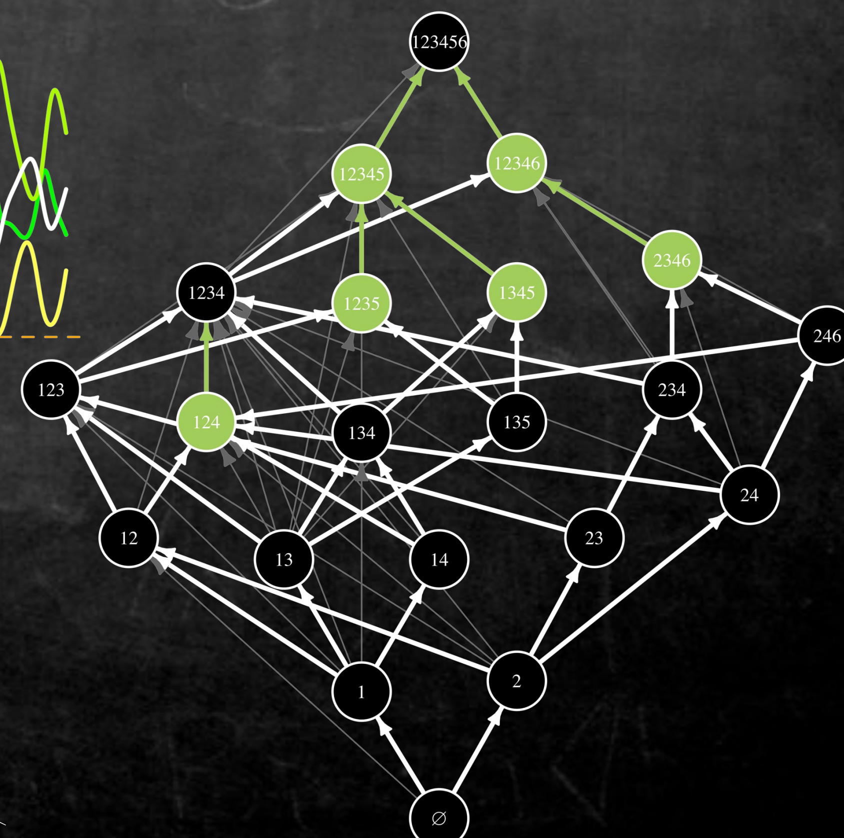
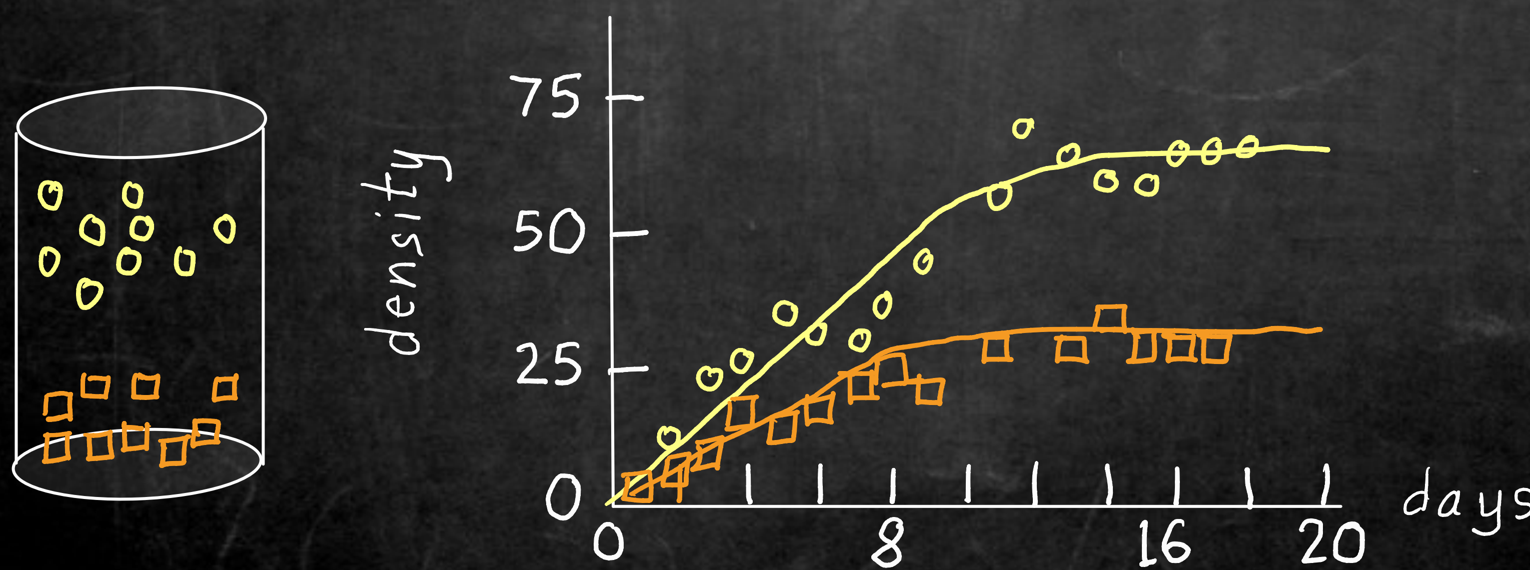
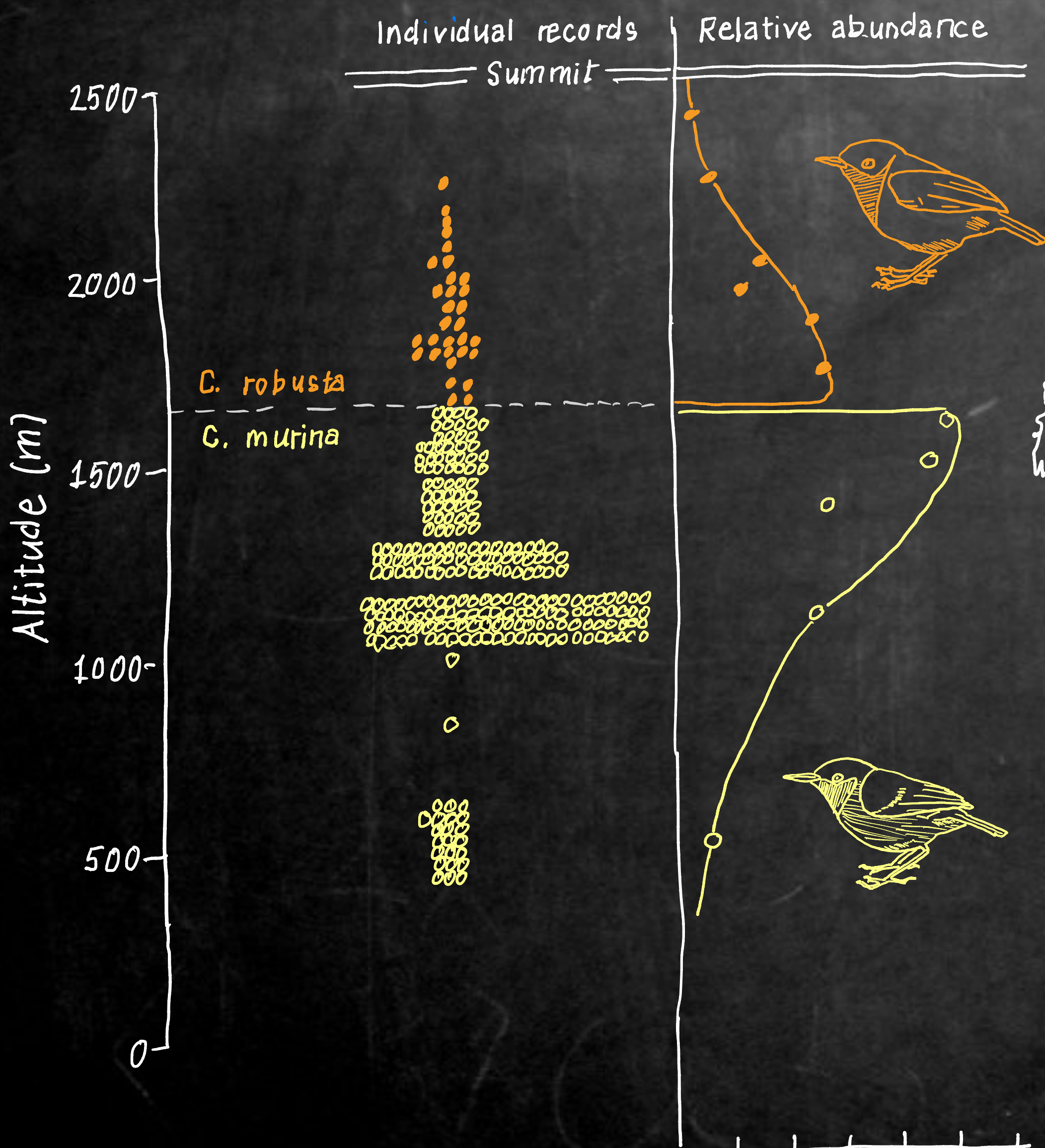




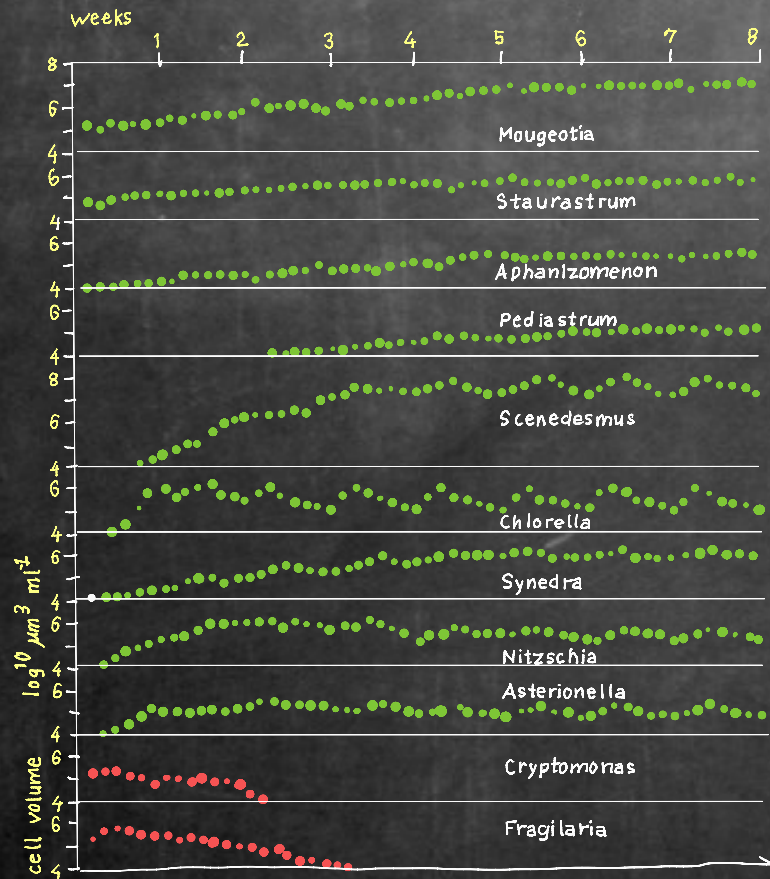




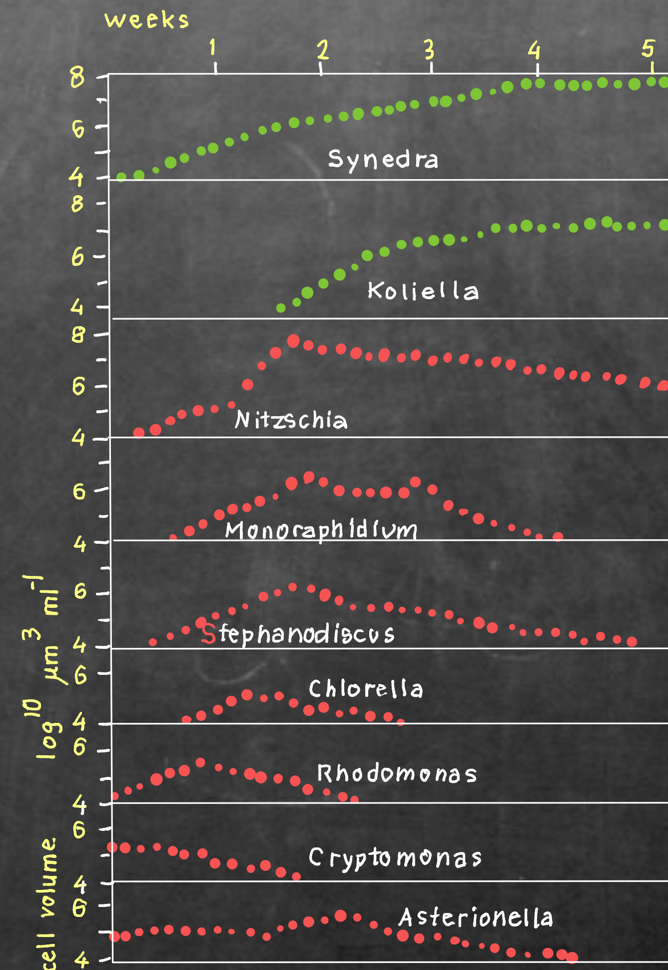
Gause 1934



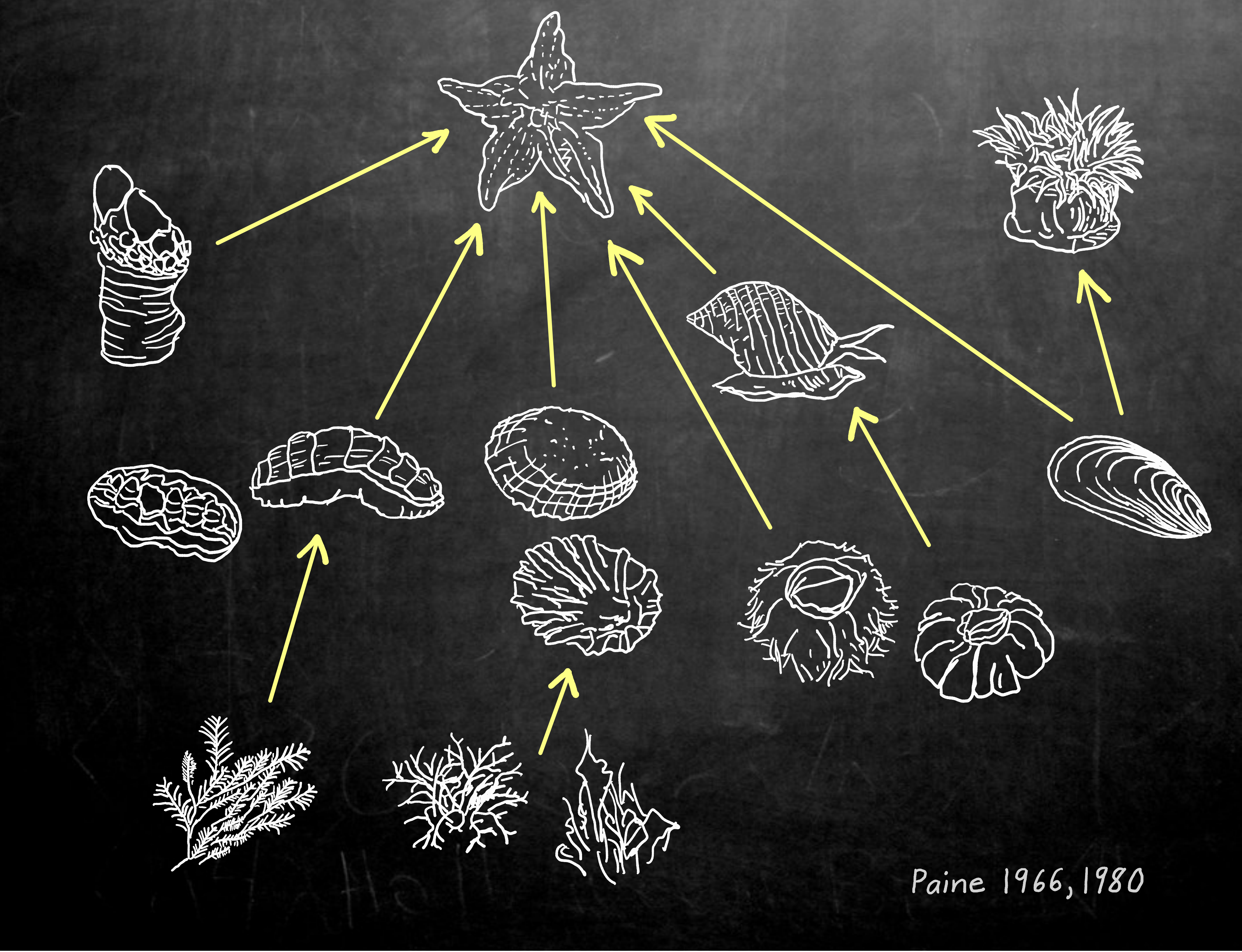
Diamond 1973

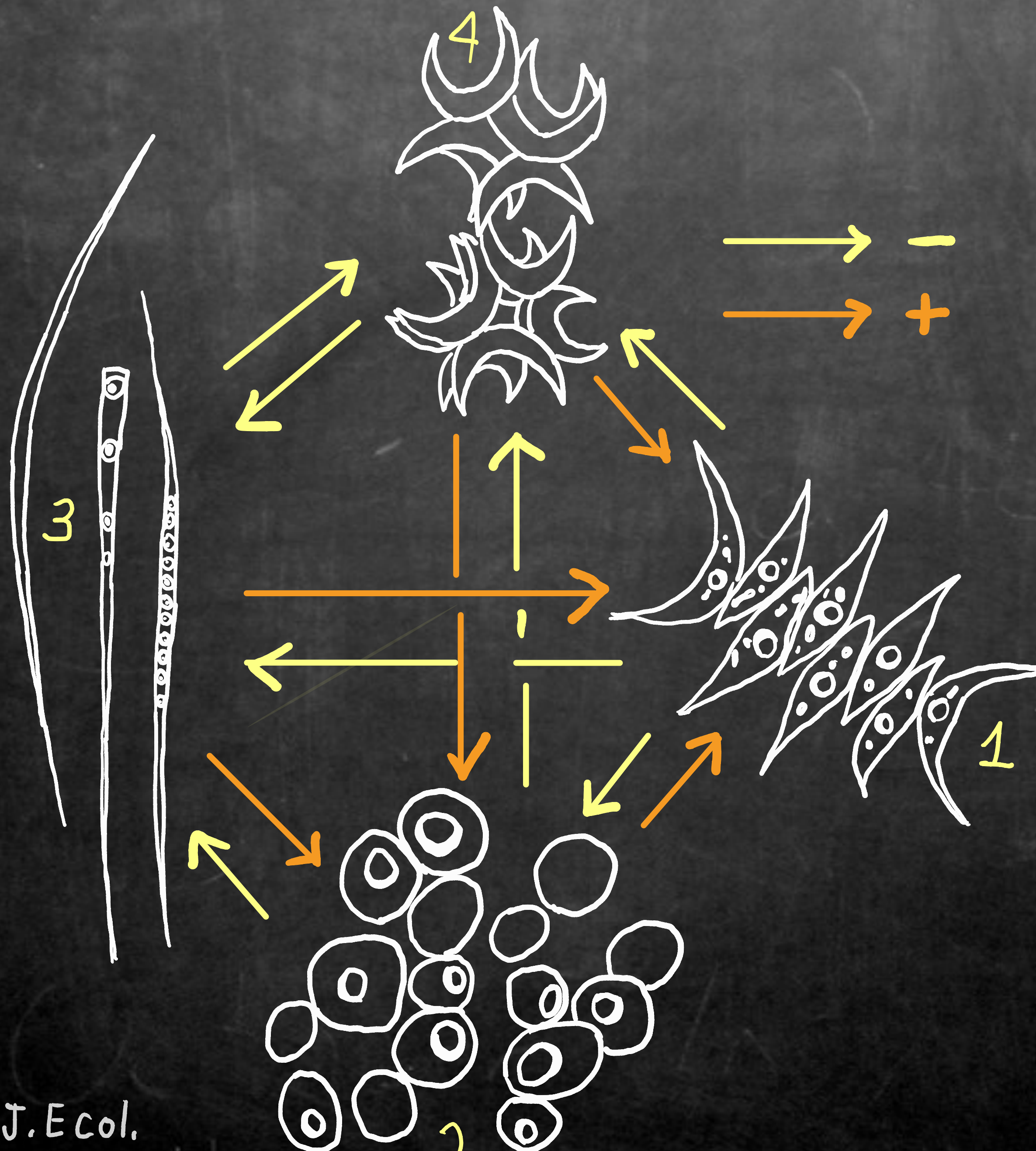


Sommer 1985



"The diversity was explained primarily by a permanent failure to acheive equilibrium as the relevant external factors changed." Hutchinson 1961

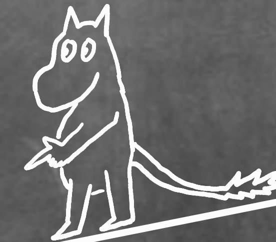

Paine 1966, 1980



Venail et al. 2014 J. Ecol.

Maynard et al. 2019 Ecol. Let.

MODERN COEXISTENCE THEORY [MCT]



"invader" species i

$r_i(S)$ = average per-capita growth rate of i when rare in community S

invasion growth rate (IGR)

"resident" community S

MODERN COEXISTENCE THEORY [MCT]

1. Positive IGRs imply coexistence

2. Decompose and compare IGRs to identify relative importance of different coexistence mechanisms

Chesson 1994, 2018; Ellner et al. 2019

Adler et al. 2006, 2009, 2010

Ellner et al. 2016, 2019

Angert et al. 2009

Sears & Chesson 2007

Shoemaker et al. 2022

Spaak et al. 2021, 2022

Blackford et al. 2022

MODERN COEXISTENCE THEORY [MCT]

1. Positive IGRs imply coexistence

"Coexistence: in the context of the invasion criterion, coexistence occurs when all competitors have positive invasion growth rates." – Grainger et al. 2019 TREE

"All species persist and coexistence is stable if all species have a positive invasion growth rate." – Ellner et al. 2019 Ecol. Let.

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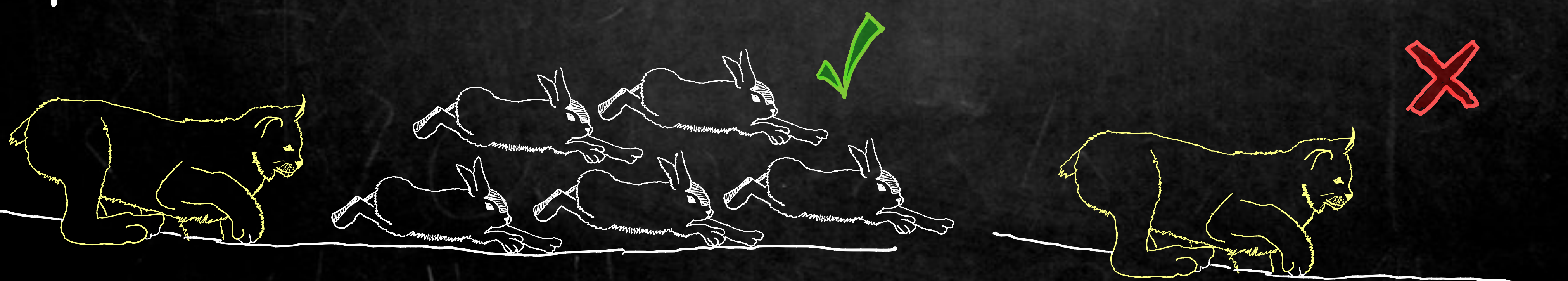
What does this mean?

positive in all contexts? No, Too restrictive



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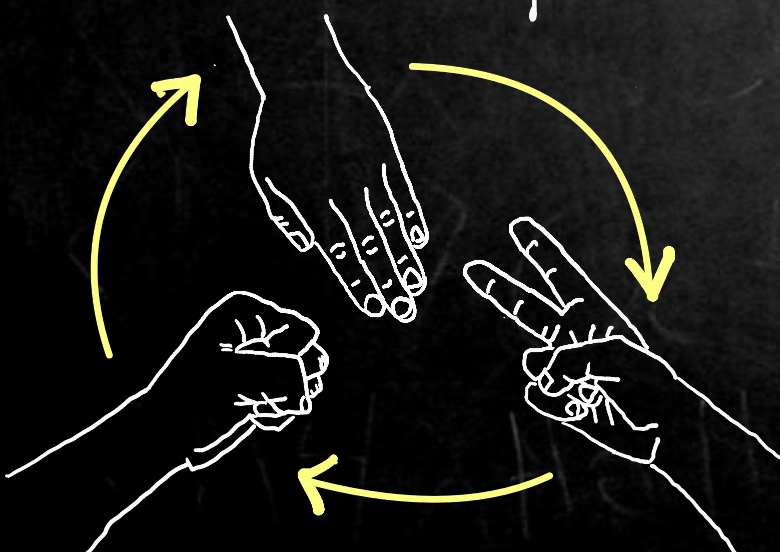
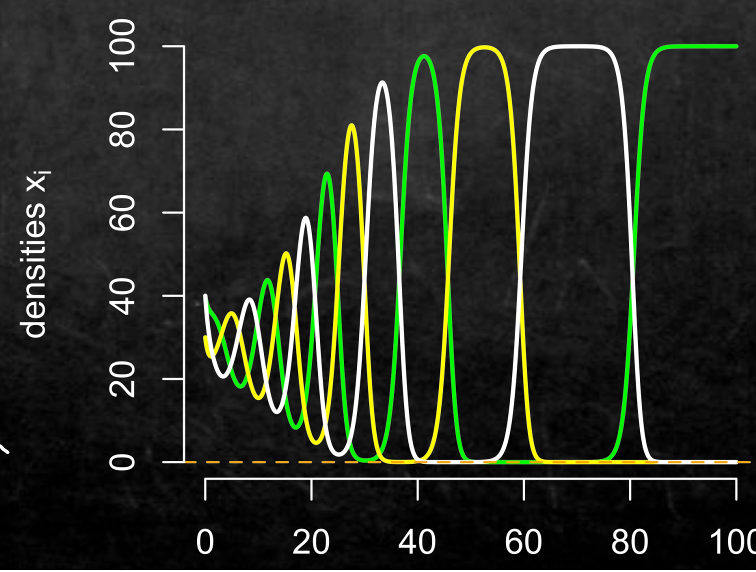
What does this mean?

at least one positive in all contexts? No, Not sufficient.





When do the signs of IGRs determine coexistence?

When they do, which IGRs need to be positive?

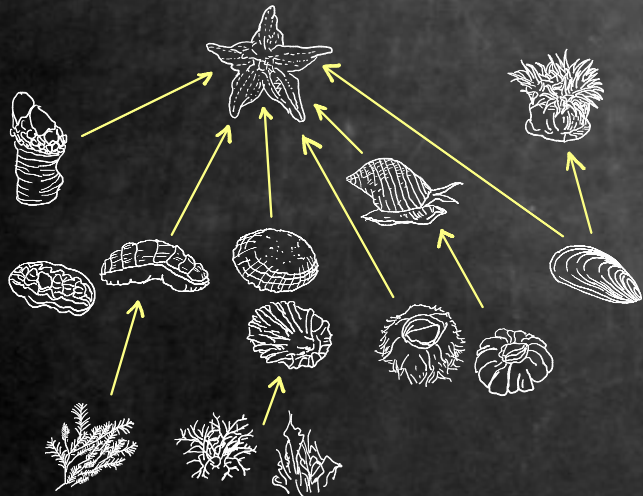
To answer these questions and more...

need to

clarify what we mean by coexistence

take advantage of some old math
[Garay 1989, Schreiber 2000]

understand community assembly

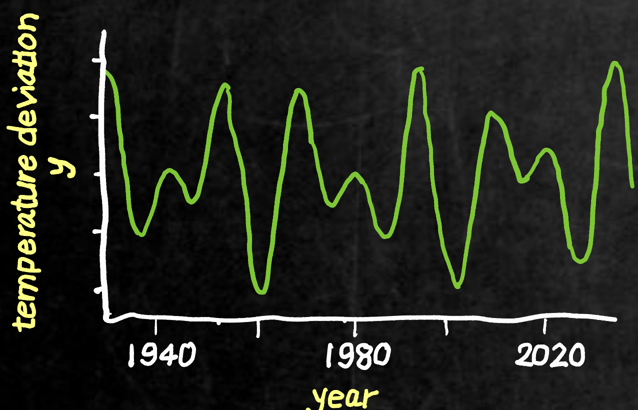


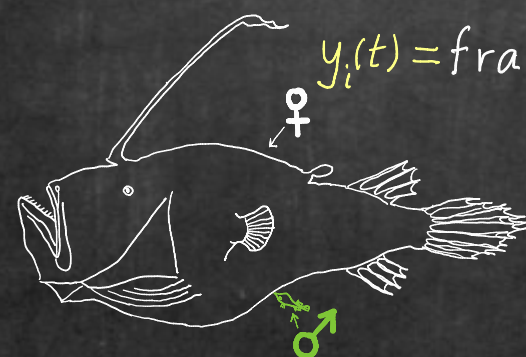
$x = (x_1, x_2, \ldots, x_n)$ spp. densities

$y = (y_1, y_2, \ldots, y_m)$ auxiliary variables

$$\frac{dx_i}{dt} = x_i f_i(x,y) \quad \frac{dy_j}{dt} = g_j(x,y)$$

auxiliary what?





$y_i(t) =$ fraction ♀

$y =$ soil characteristics

for this talk focus on Lotka-Volterra models

$$f_i(x) = r_i + \Sigma_j a_{ij} x_j$$

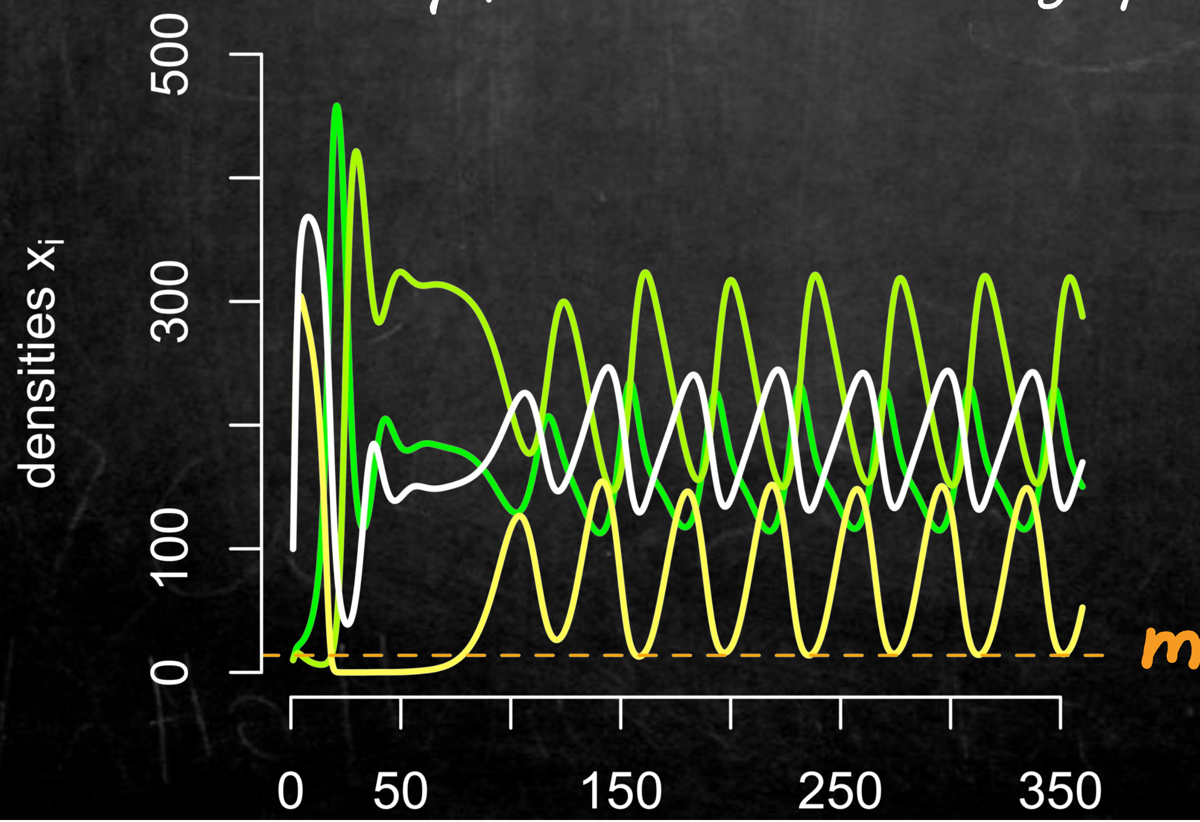
check out Hofbauer & Schreiber 2022 ArXiv for general case

What is meant by coexistence?

Several alternatives e.g. positive stable equilibrium
positive attractor

For IGR approaches, most sensible is

permanence: there is a minimal density $m>0$ such that all spp. densities exceed m after enough time & whenever all spp. are initially present



A set $S \subseteq \{1, 2, \ldots, n\}$ of species is a **realized subcommunity** if there is an equilibrium at which only their densities are >0

[ergodic measure $\mu(dx, dy)$]

community S

rare species i

$r_i(S) =$ average per-capita growth rate of i at equilibrium supporting S

$[= f_i(\hat{x}_S)$ or $= \int f_i(x,y)\,\mu(dx,dy)]$

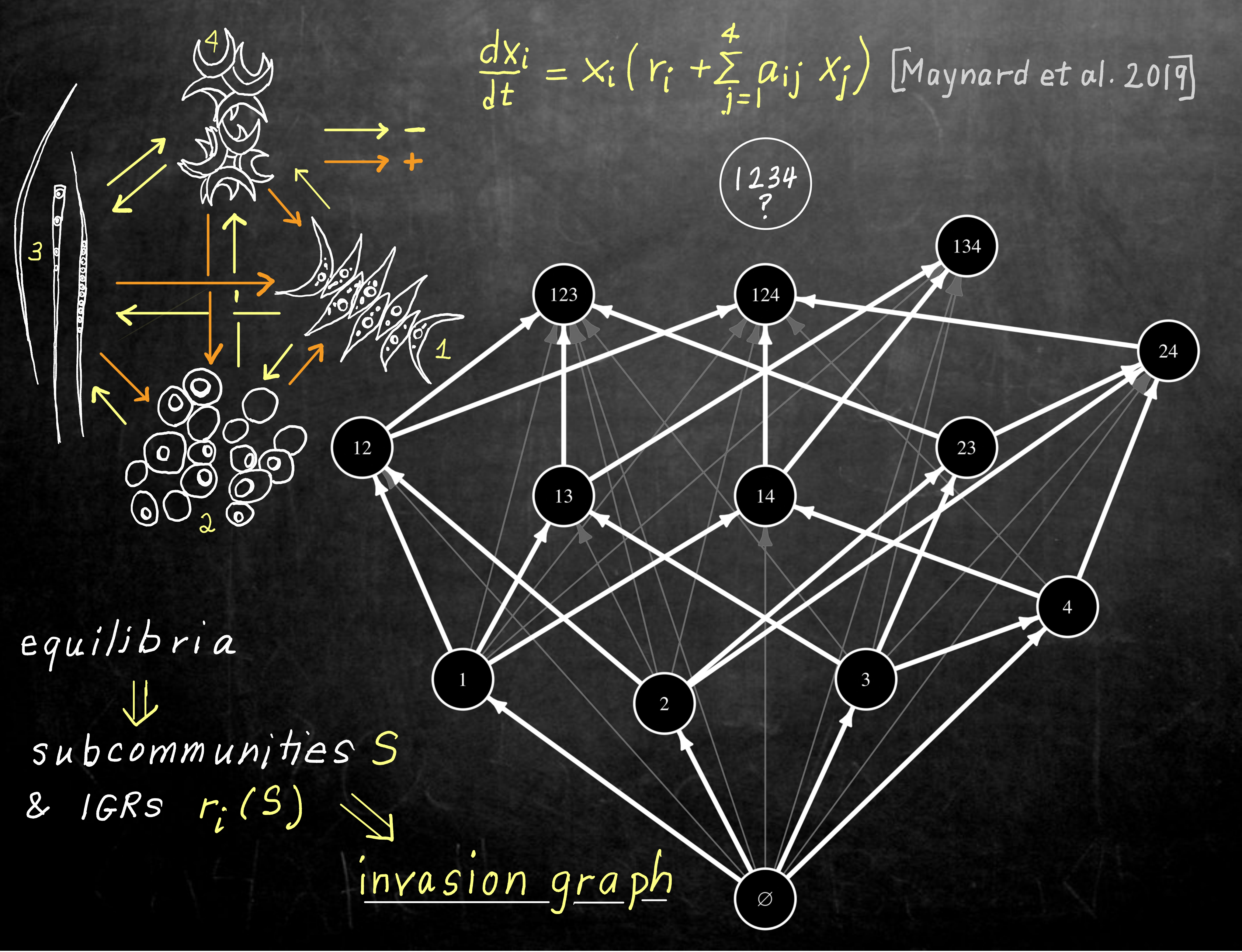
invasion growth rate (IGR)

A set $S \subseteq \{1, 2, \ldots, n\}$ of species is a realized subcommunity if there is an equilibrium at which only their densities are >0

[ergodic measure $\mu(dx)$]

the invasion graph: a graph whose vertices correspond to realized subcommunites and $S \longrightarrow T$ if ...


$r_j(T)<0$
$r_i(S)>0$
community T
community S



$\frac{dx_i}{dt} = x_i(r_i + \sum_{j=1}^{4} a_{ij} x_j)$
[Maynard et al. 2019]
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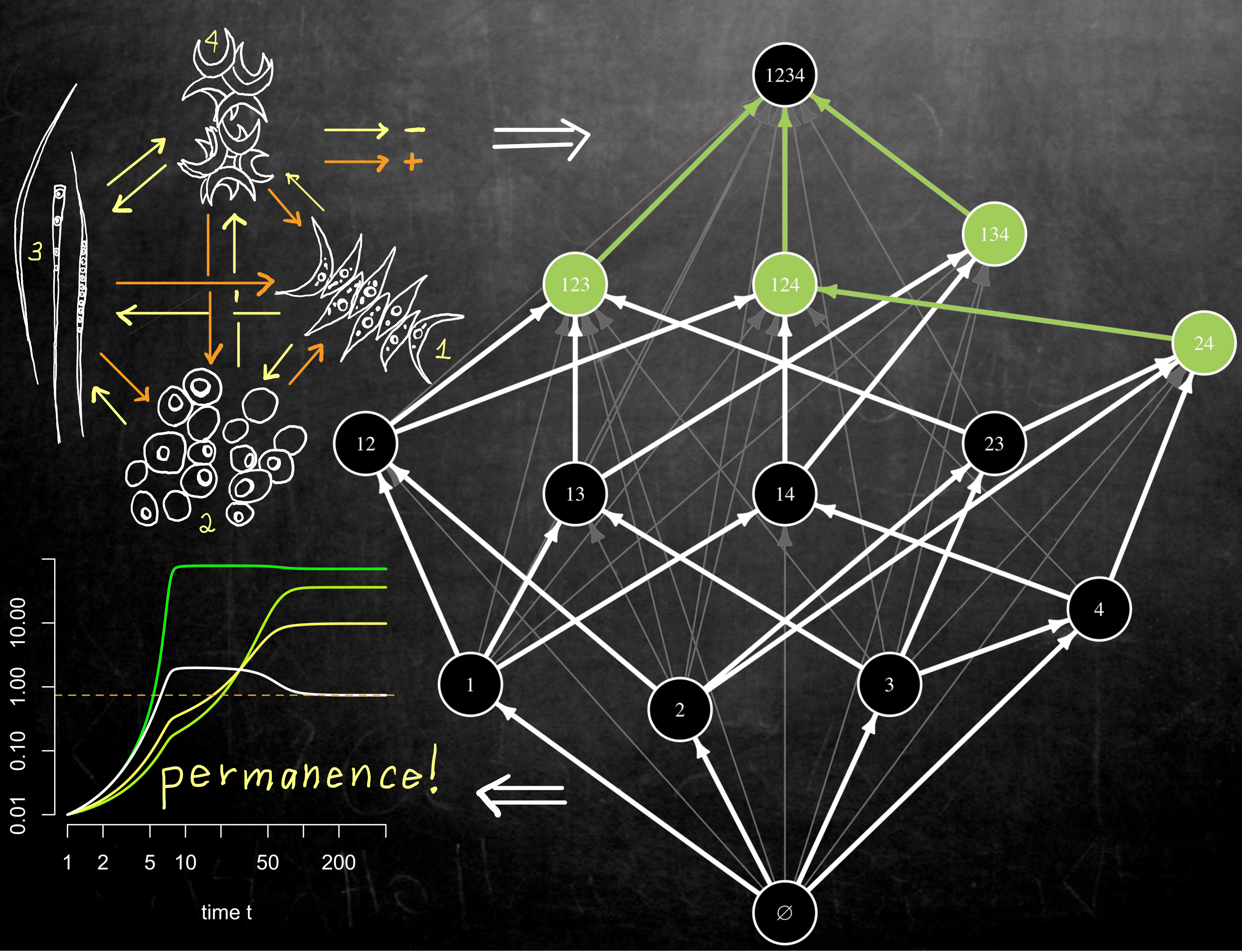
subcommunities S
& IGRs $r_i(S)$
invasion graph

an invasion graph is acyclic if there no sequence of invasion starting and ending at the same subcommunity

a community $S \subseteq \{1, 2, 3, \dots, n\}$ is a $-i$ community if it doesn't include i and $r_j(S) \leq 0$ for all $j \neq i$ [cf. Chesson 1994]

Theorem [Hofbauer & Schreiber 2022]

If the invasion graph is acyclic, then all spp. coexist if and only if $r_i(S) > 0$ for all $-i$ communities S



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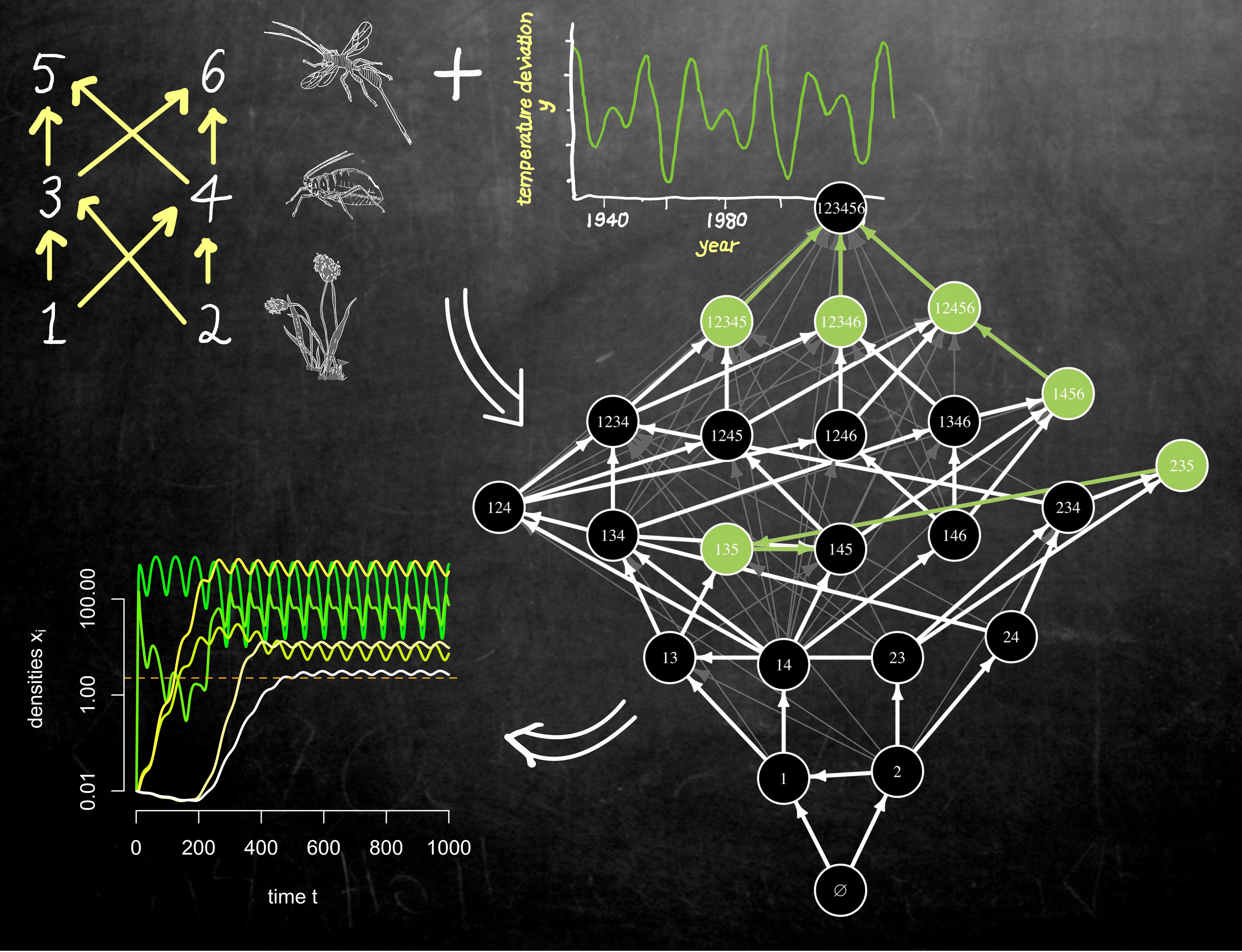

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densities x_i
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1.00
0.01
0
200
400
600
800
1000
time t

Positive IGRs imply coexistence

When are the signs enough?

when the invasion graph is acyclic

Which need to be positive?

only the IGRs of spp i at $-i$ communities

What next?

deal with cyclic invasion graphs

use invasion graphs and classical MCT to understand mechanisms underlying end states of community assembly (w/ Jürg Spaak)