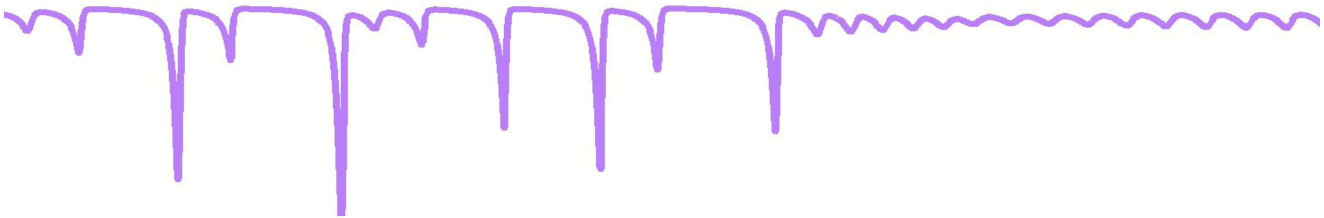
# Evolution of dormancy in the context of complex ecological dynamics



Zach Miller | Yale University | October 2024

# Dormancy

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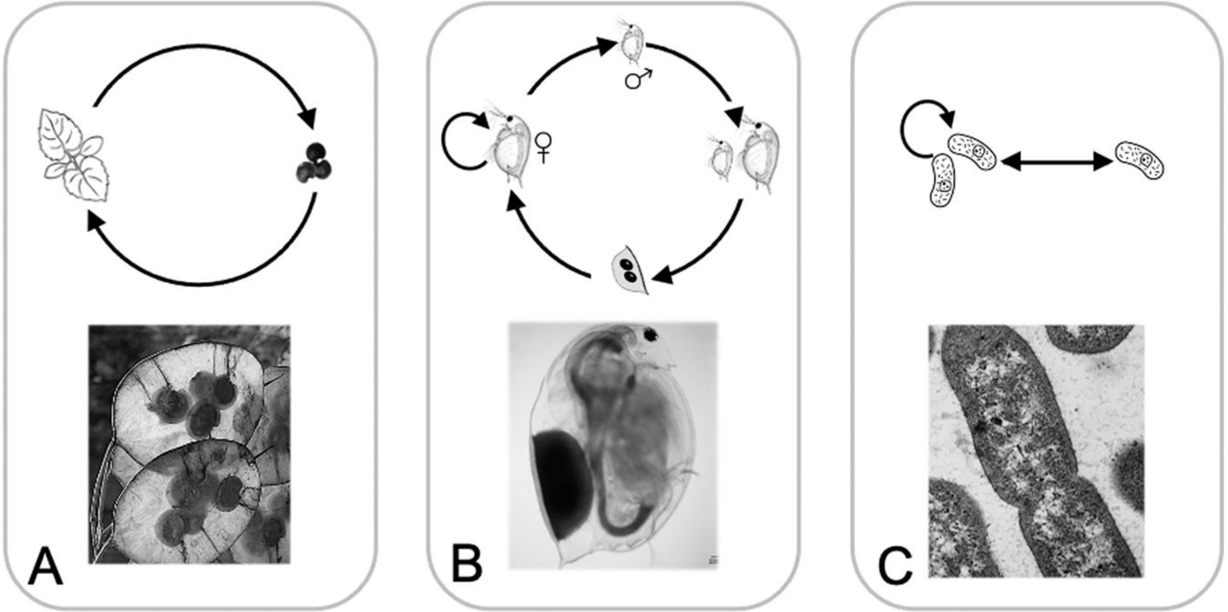


Lennon et al. (2021)
Nature Comm.

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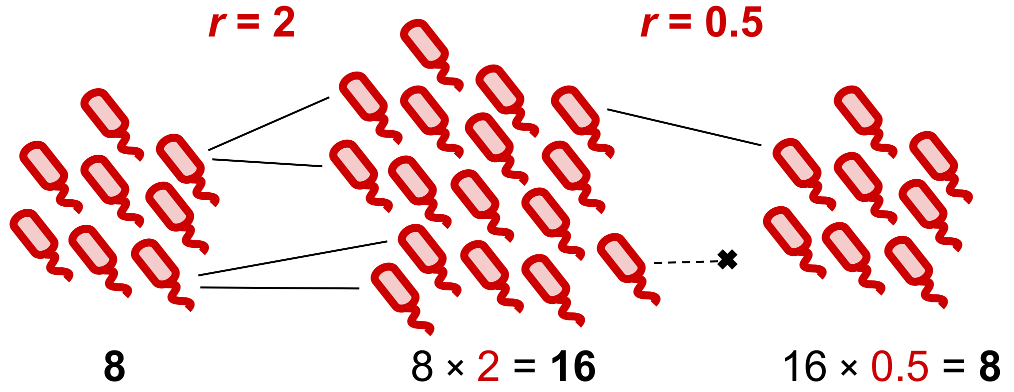
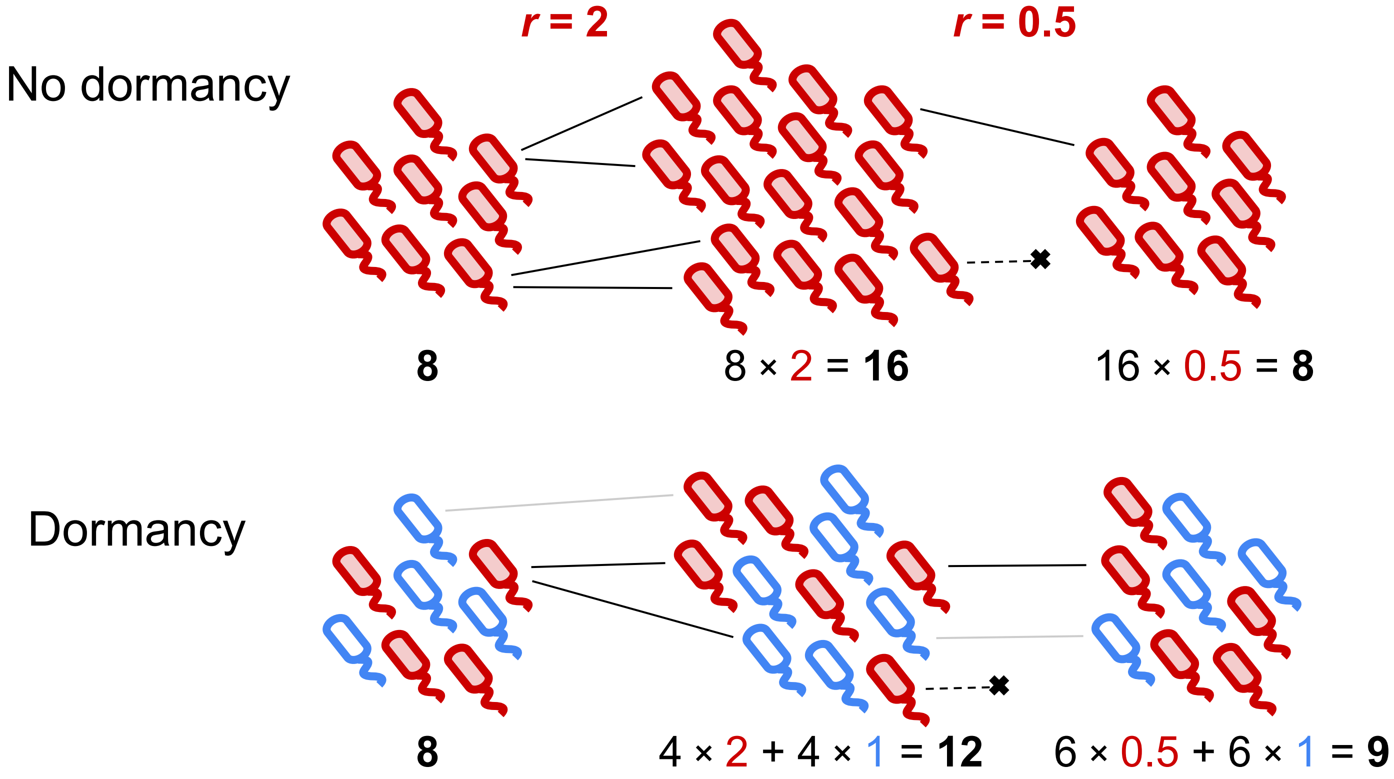
- Adaptive strategy in variable environments
- In predictable environments, dormancy can be used to avoid stressors
  - e.g. seasonal diapause, sporulation in response to stress
- In unpredictable environments, dormancy can still be adaptive as a **bet-hedging strategy** (Cohen 1966)
  - Bet-hedging increases long-run growth by reducing temporal variance in growth rates

# Dormancy as a bet-hedging strategy

No dormancy



# Dormancy as a bet-hedging strategy



# Extrinsic variability

- Temperature
- Precipitation
- Resource pulses
- …

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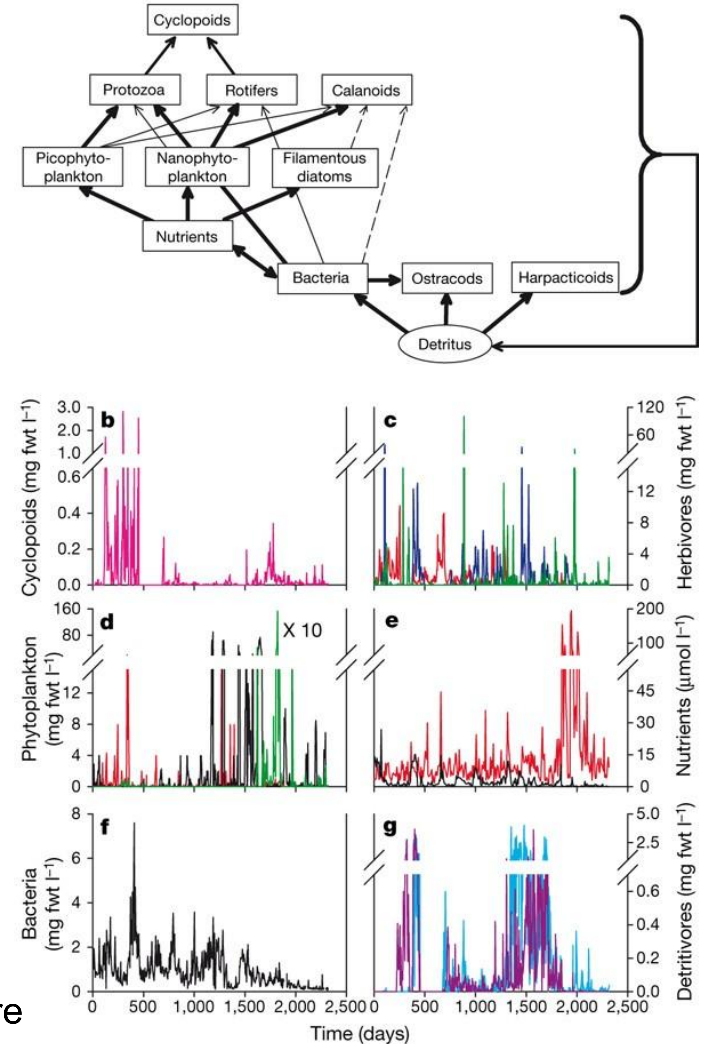
## Intrinsic variability

# Endogenous fluctuations in population dynamics

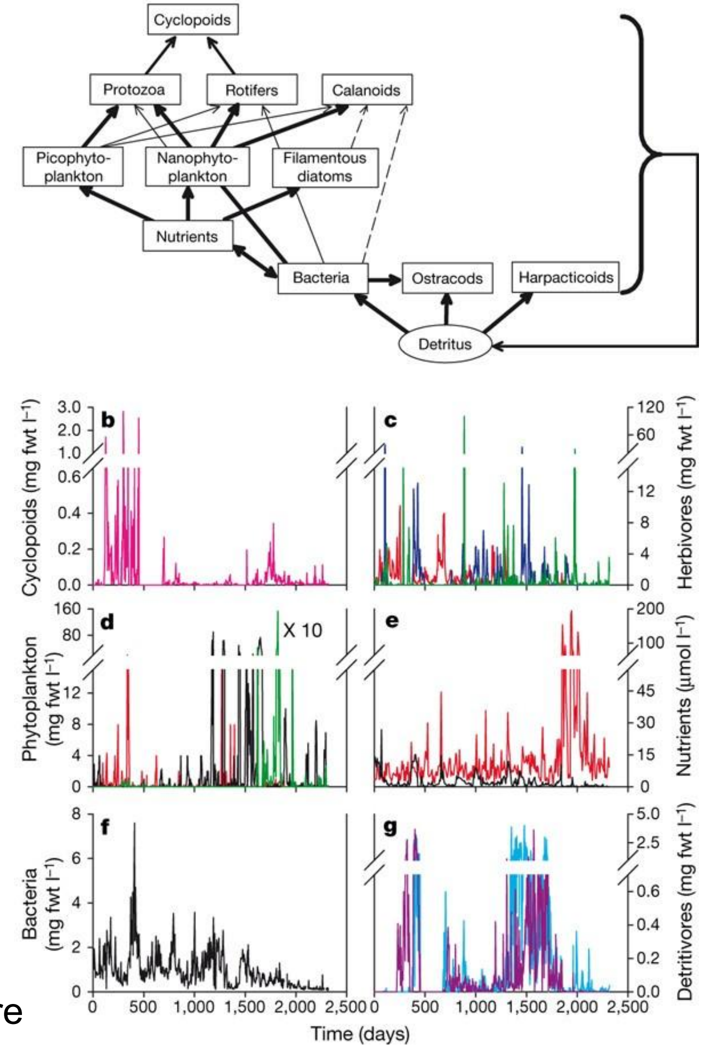
- Strong interactions can lead to population cycles and chaos

Beninca et al. (2008) Nature



# Endogenous fluctuations in population dynamics

- Strong interactions can lead to population cycles and chaos
- Theoretical models predict cycles and chaos should be very common
  - Especially in trophic systems




Beninca et al. (2008) Nature

# Endogenous fluctuations in population dynamics

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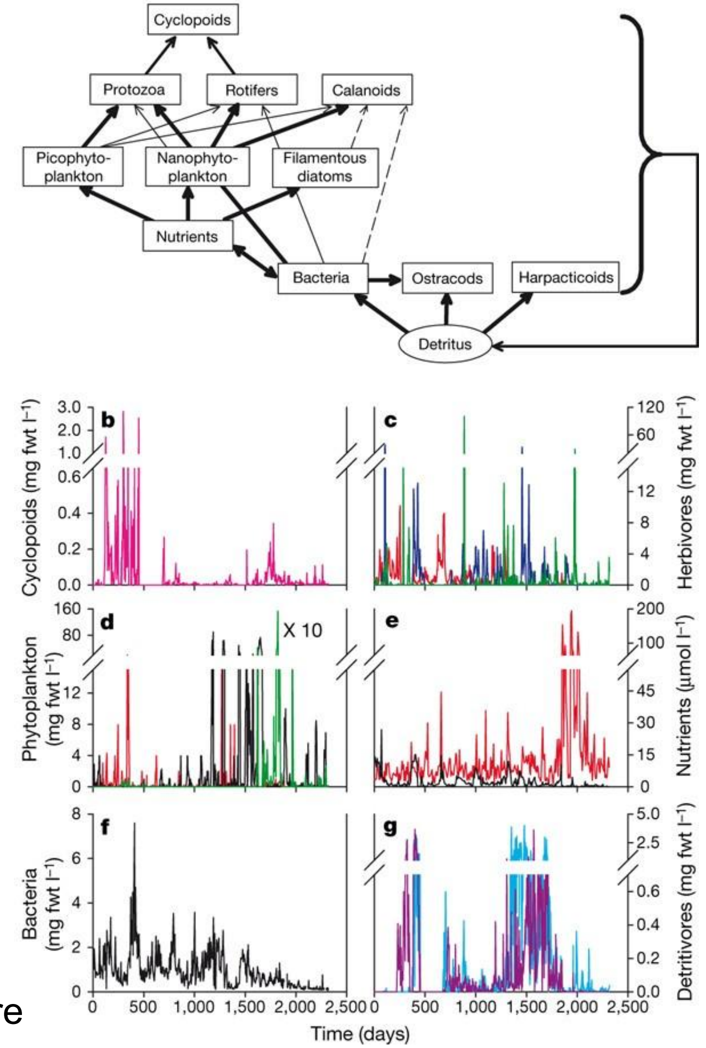
- Theoretical models predict cycles and chaos should be very common
  - Especially in trophic systems
- Two big questions: Are cycles and chaos rare in nature? If so, why?




Beninca et al. (2008) Nature

# Dormancy in the context of complex ecological dynamics

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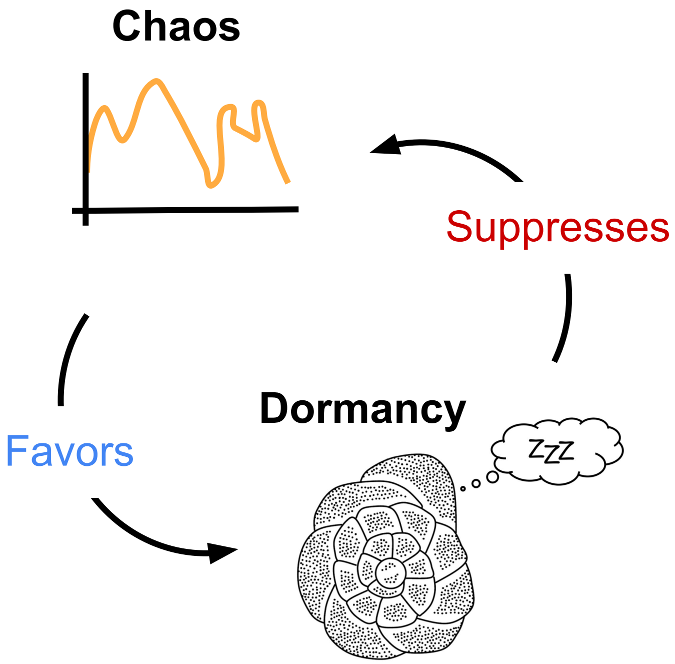
- Is dormancy an adaptive strategy in the presence of population cycles/chaos?
- How does dormancy affect population dynamics?
- **How does feedback between dormancy and stability play out?**




Glock (2023)
Biogeosciences

## Extrinsic variability

- Temperature
- Precipitation
- Resource pulses
- …

## Intrinsic variability

**Overcompensation in discrete time population dynamics**
**(pre-print online now)**

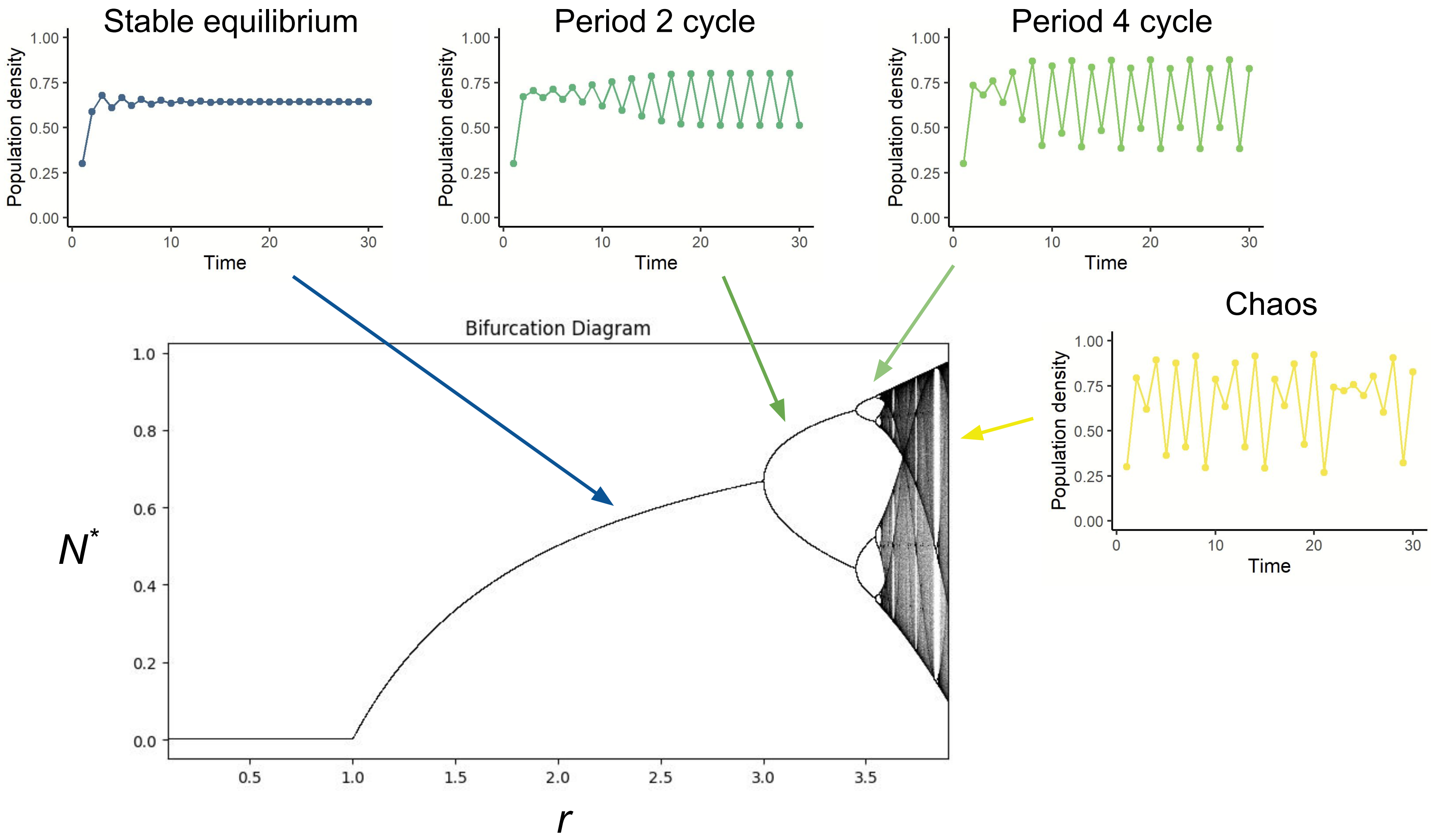
# Chaos in 1-D discrete-time population dynamics

- Many well-known discrete-time models exhibit chaos
  - e.g. Ricker, Hassel, Maynard-Smith models
- A simple “archetype” for this behavior is the discrete-time logistic growth model:

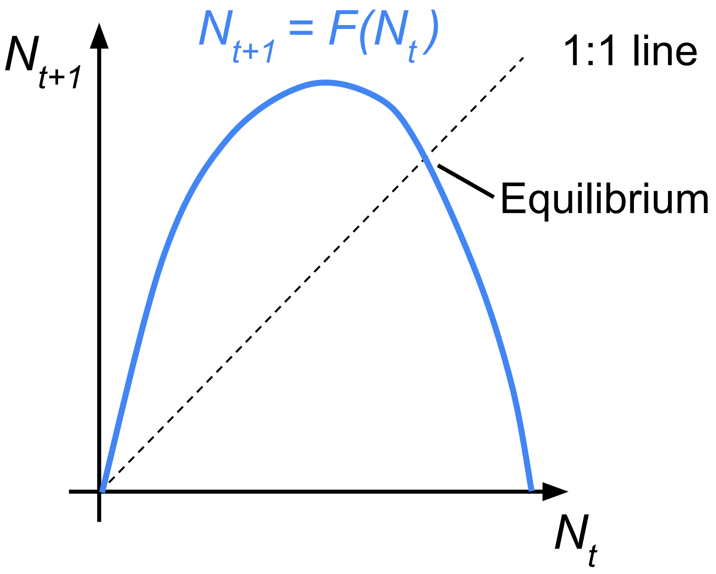
$$N_{t+1} = rN_t(1 - N_t)$$

Intrinsic growth rate

Density dependence


Stable equilibrium
Period 2 cycle
Period 4 cycle
Chaos
Population density
Time
1.00
0.75
0.50
0.25
0.00
0
10
20
30
Bifurcation Diagram
1.0
0.8
0.6
0.4
0.2
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
$N^*$
$r$

# The origins of instability



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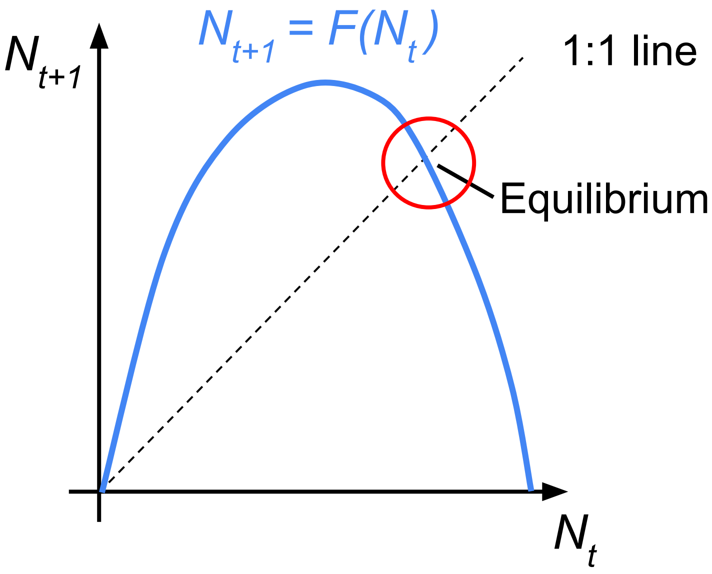
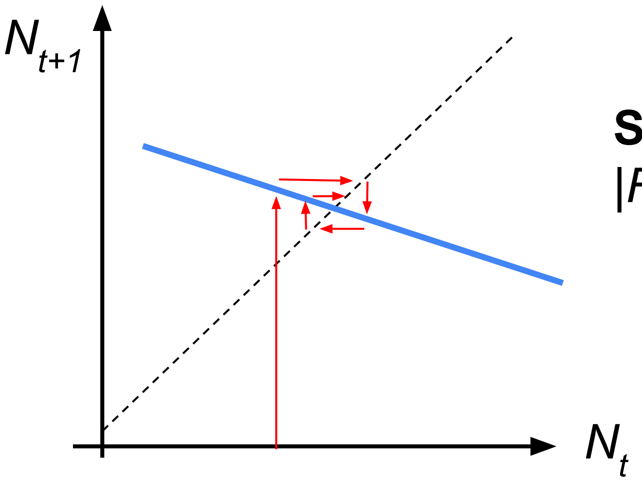
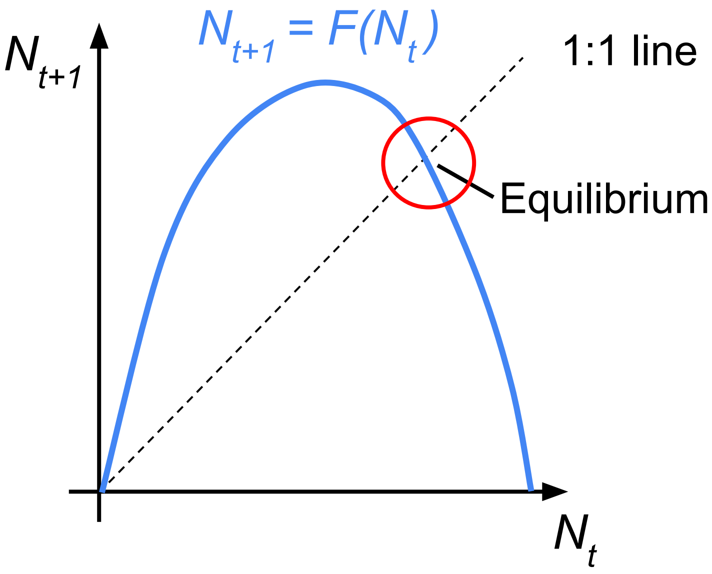


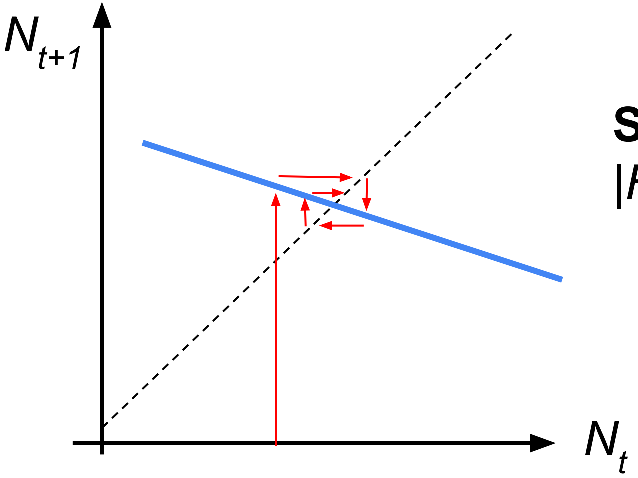




**Stable**

$|F'(N^*)| < 1$

# The origins of instability

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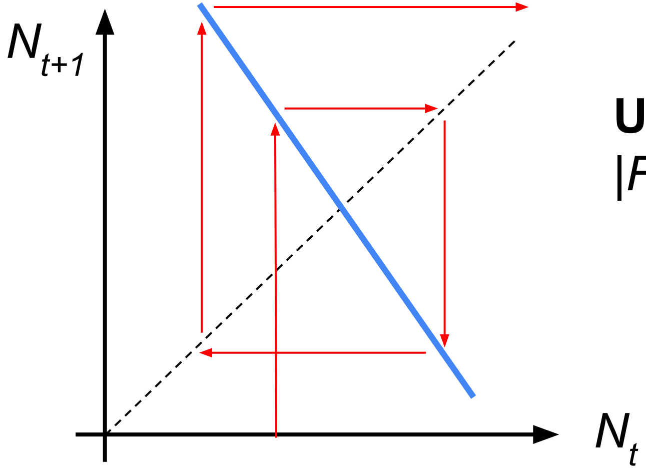


**Unstable**
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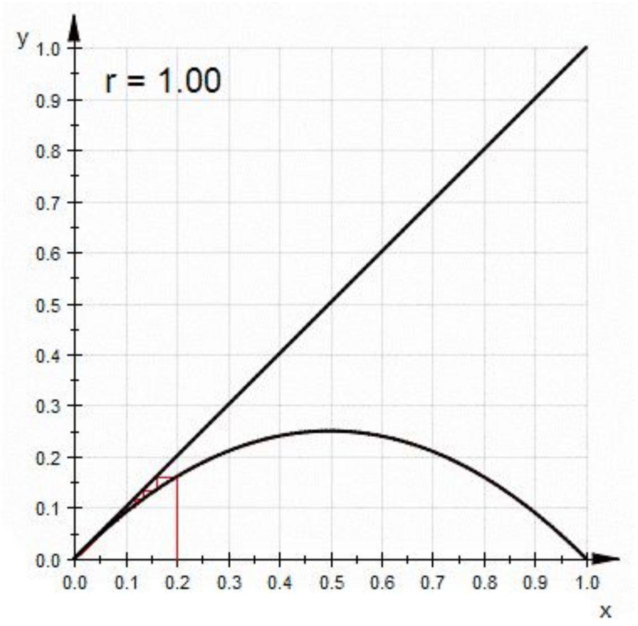
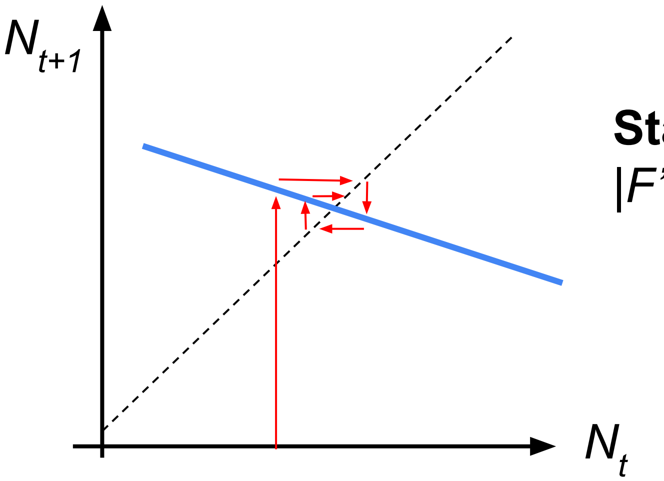
# The origins of instability




Sam Derbyshire (Wikipedia)

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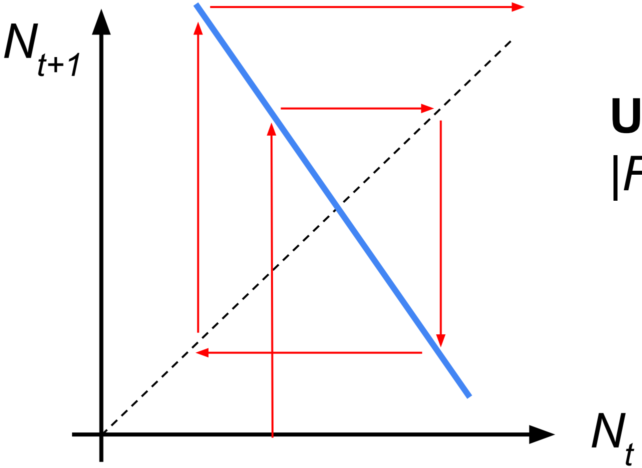


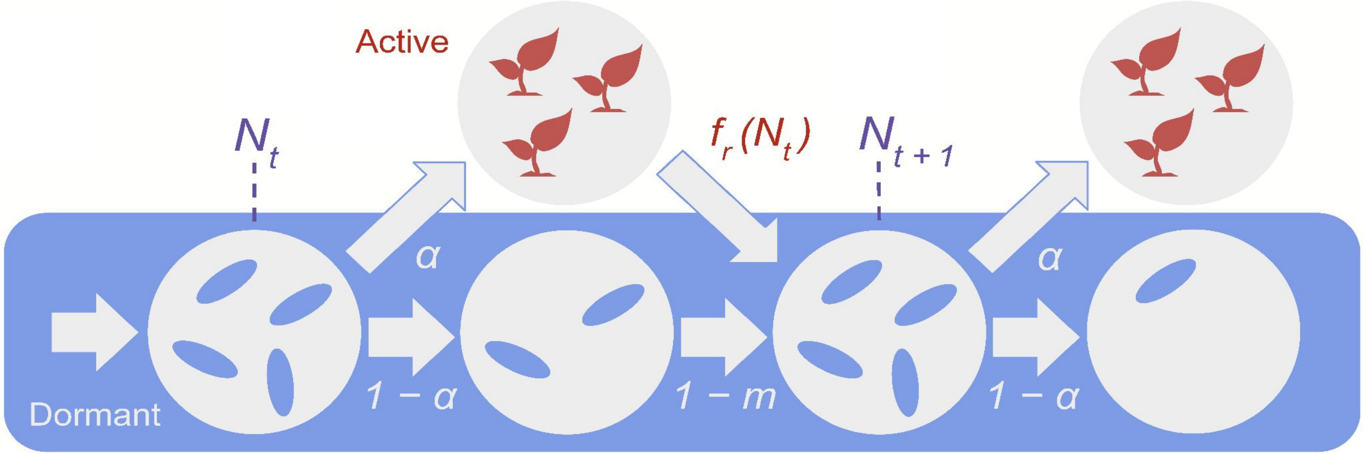

**Unstable**

$|F'(N^*)| > 1$

# Adding dormancy

Density-dependent growth — Dormant fraction — Mortality in dormancy

$$N_{t+1} = \alpha\, N_t\, \underbrace{f(\alpha\, N_t)}_{\text{Density-dependent growth}} + \underbrace{(1-\alpha)}_{\text{Dormant fraction}}\underbrace{(1-m)}_{\text{Mortality in dormancy}} N_t$$



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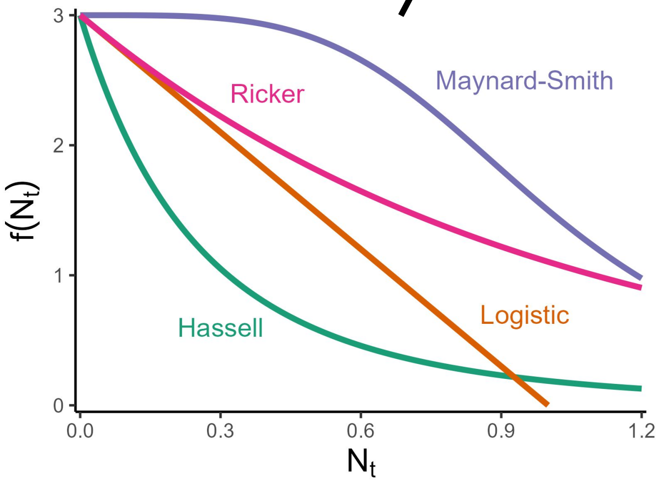


Separability: $f_r(N) = h(r)\, g(N)$
with *h* increasing, *g* decreasing

Stable equilibrium for $r < r_c$,
fluctuating dynamics for $r > r_c$

# Four results

1) Dormancy stabilizes dynamics by lowering the effective growth rate
2) Dormancy is favored when population dynamics fluctuate
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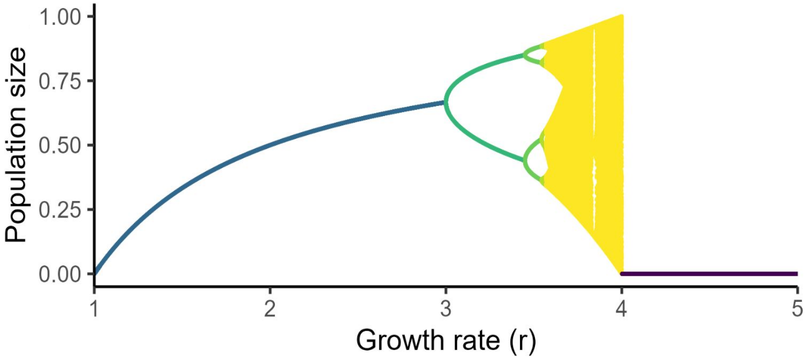
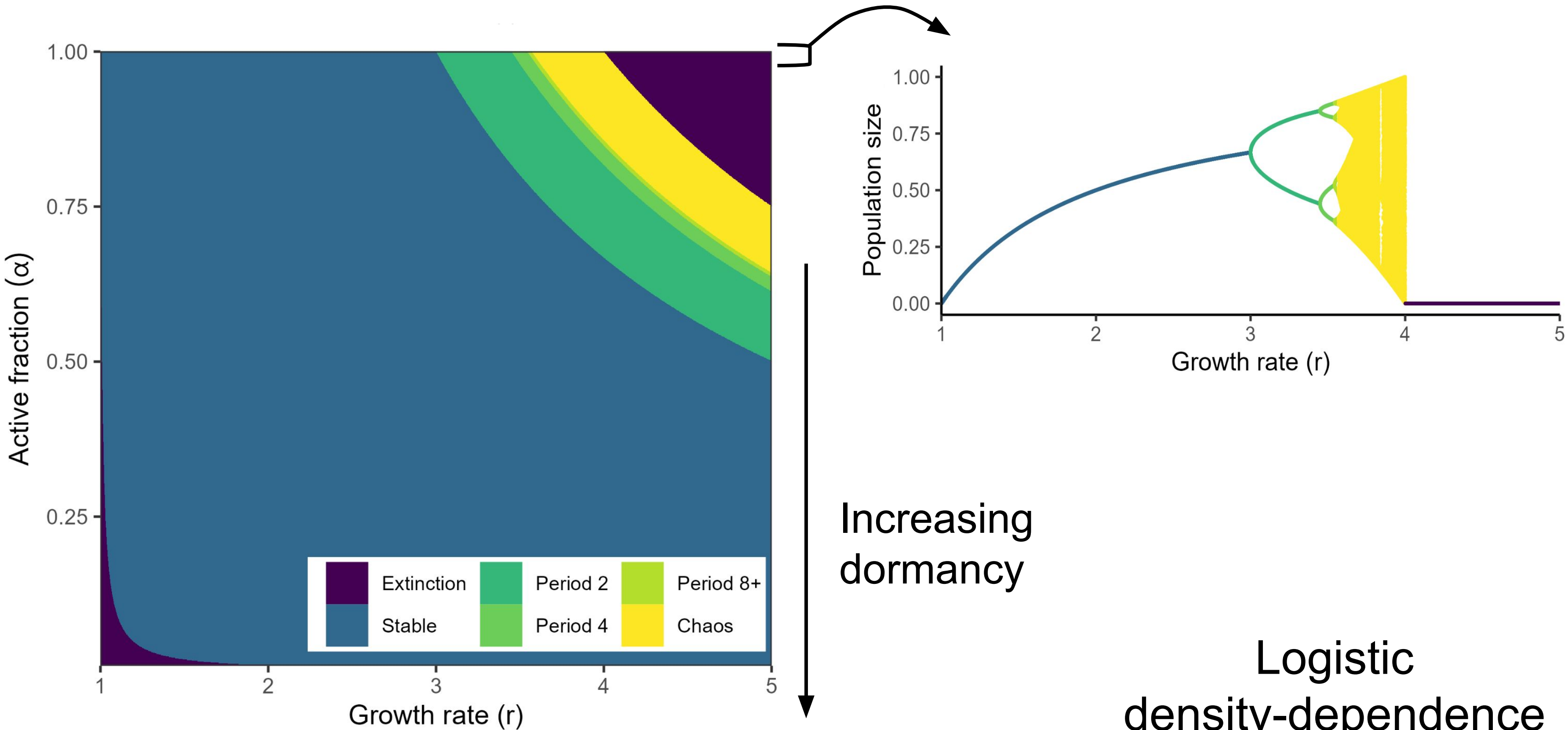
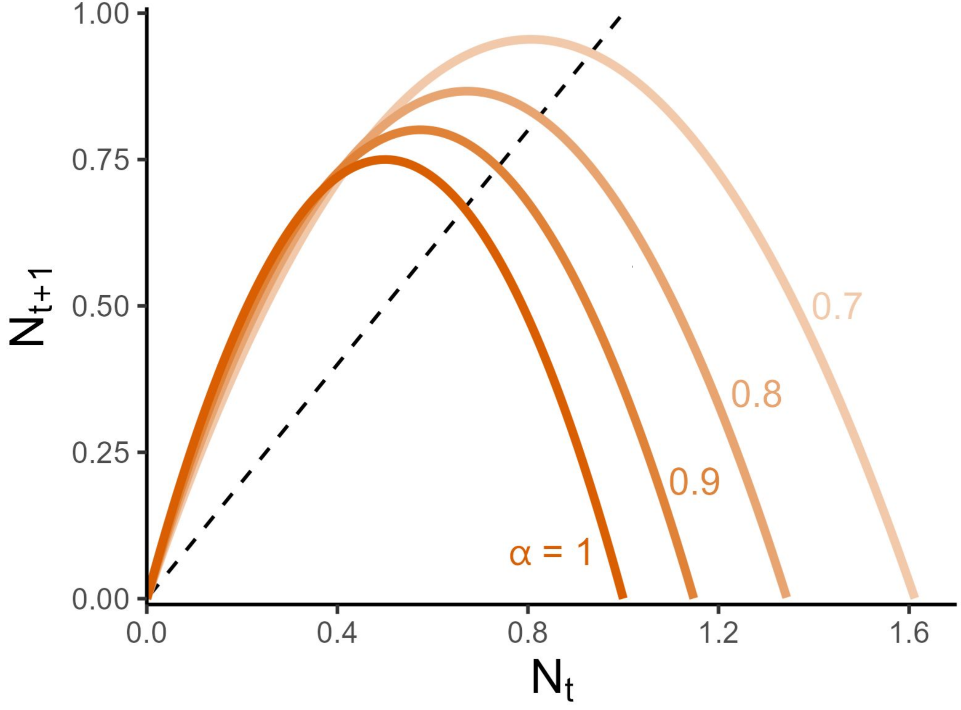

Population size
1.00
0.75
0.50
0.25
0.00
1
2
3
4
5
Growth rate (r)


1.00
0.75
0.50
0.25
Active fraction (α)
1
2
3
4
5
Growth rate (r)
Extinction
Stable
Period 2
Period 4
Period 8+
Chaos
Increasing
dormancy
Population size
1.00
0.75
0.50
0.25
0.00
1
2
3
4
5
Growth rate (r)
Logistic
density-dependence

# The origins of stabilization



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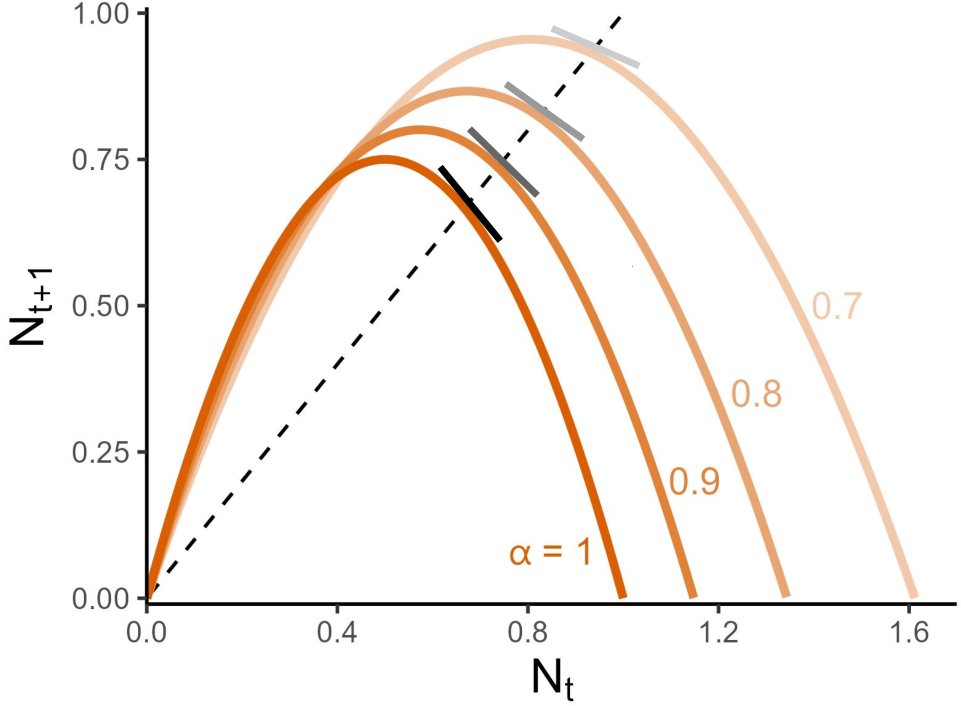

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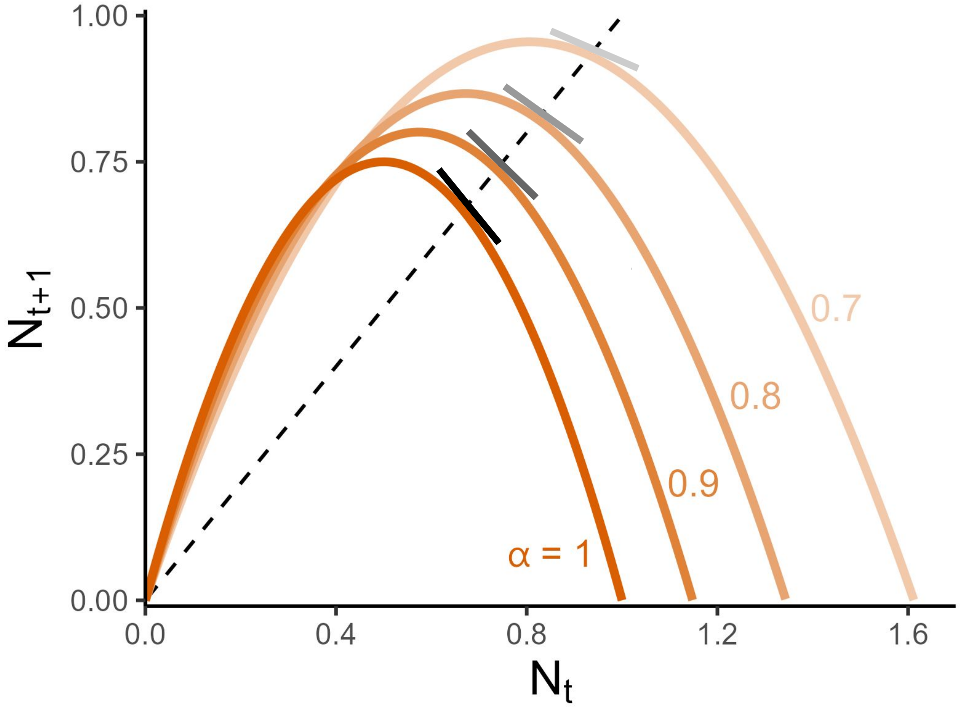


For logistic density-dependence, dynamics map onto logistic model without dormancy, according to:

$$r_{\text{eff}} = \alpha\, r + (1-\alpha)(1-m)$$

More generally, the bifurcation point increases:

$$r_c(\alpha) \geq \left(1 + \tfrac{1-\alpha}{\alpha}\, m\right) r_c(1)$$

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# Two-strategy model

$$N_{t+1} = (\alpha f_r(\alpha N_t + \alpha' N_t') + (1-\alpha)(1-m))N_t$$

$$N_{t+1}' = (\alpha' f_r(\alpha N_t + \alpha' N_t') + (1-\alpha')(1-m))N_t'$$

# Two-strategy model

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**No "niche differences"**

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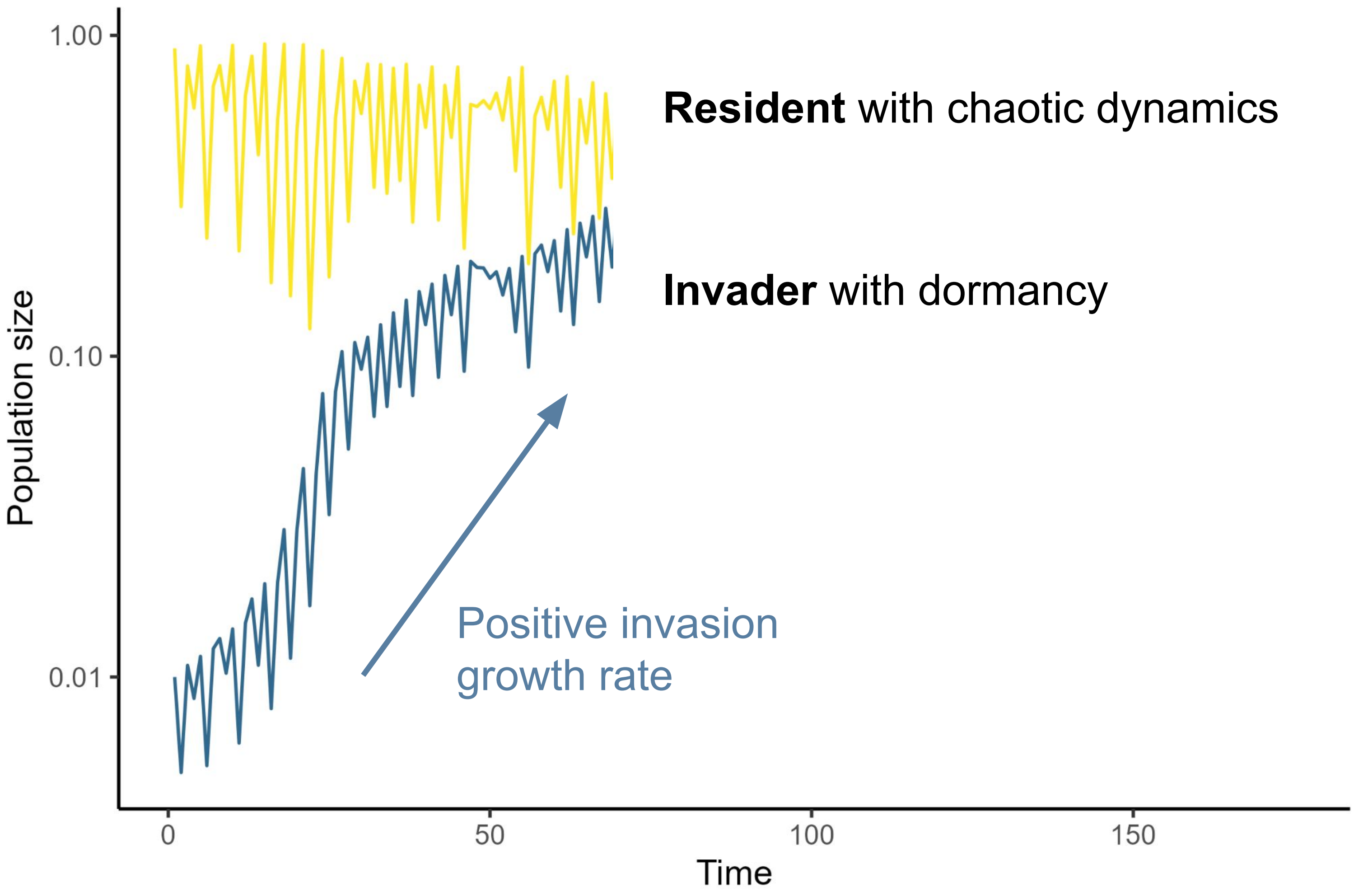
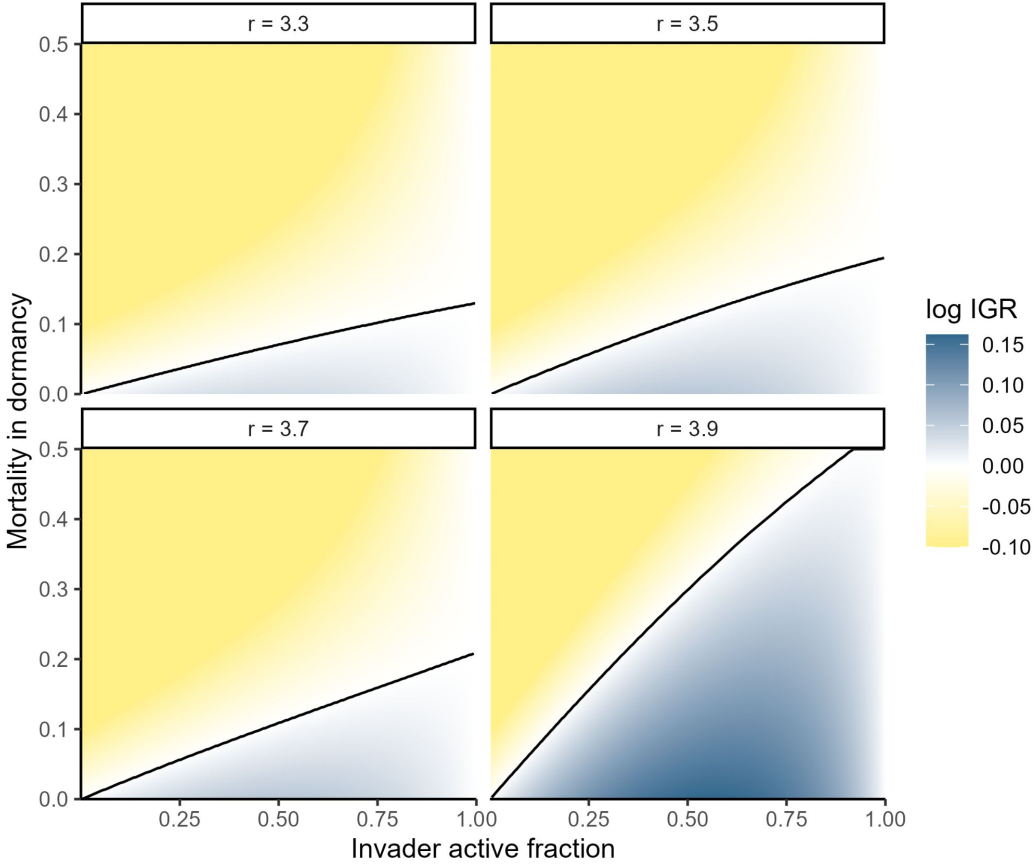
**No "niche differences"**

**Equal mortality risk in dormancy**



1.00
0.10
0.01
Population size
0
50
100
150
Time
**Resident** with chaotic dynamics
**Invader** with dormancy
Positive invasion growth rate

- Fluctuations confer a bet-hedging benefit to dormancy
  - Nonlinear averaging over high and low growth rates
- Mortality in dormancy imposes a cost
- Positive IGR when benefits > costs



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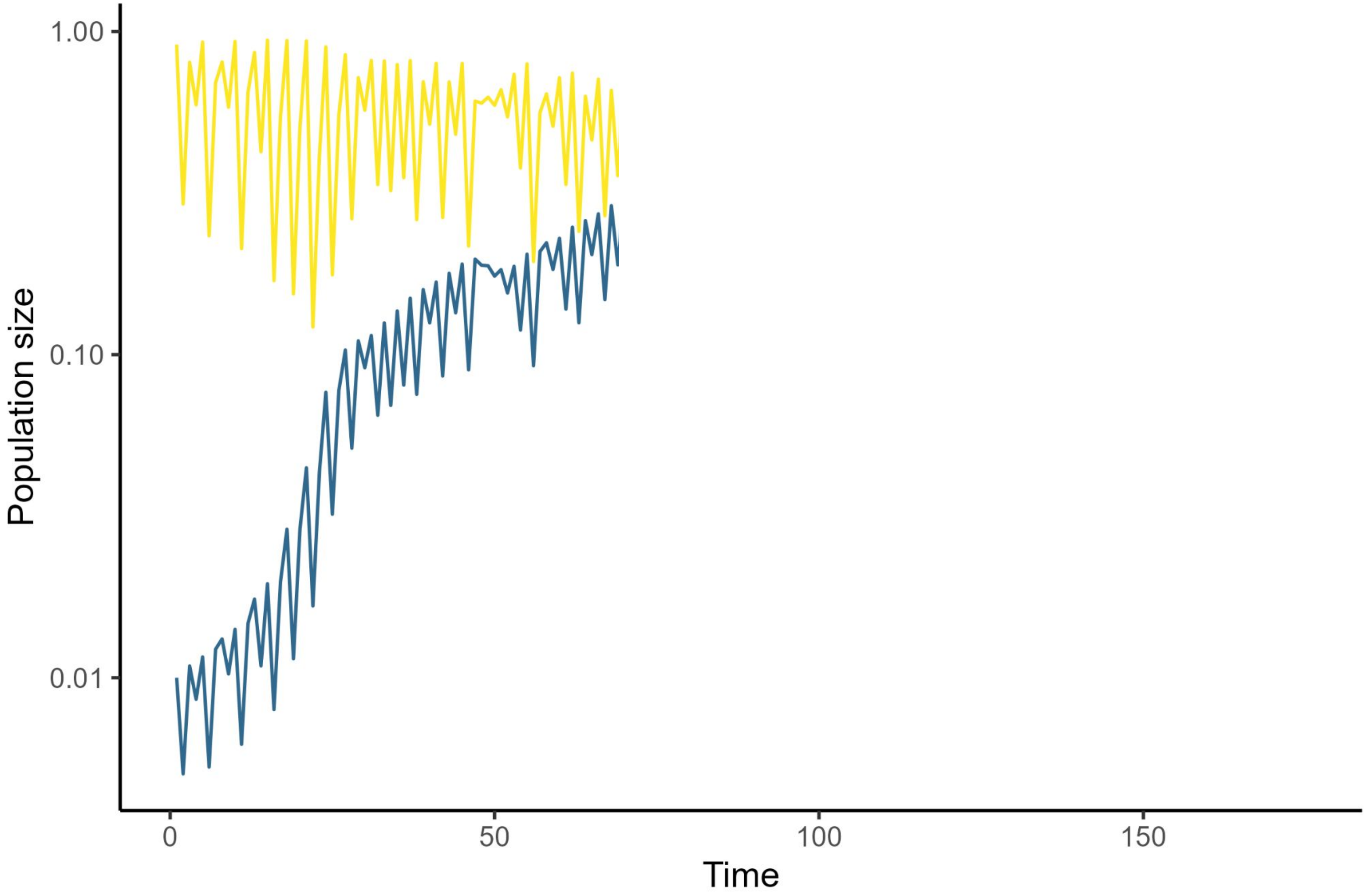
1.00
0.10
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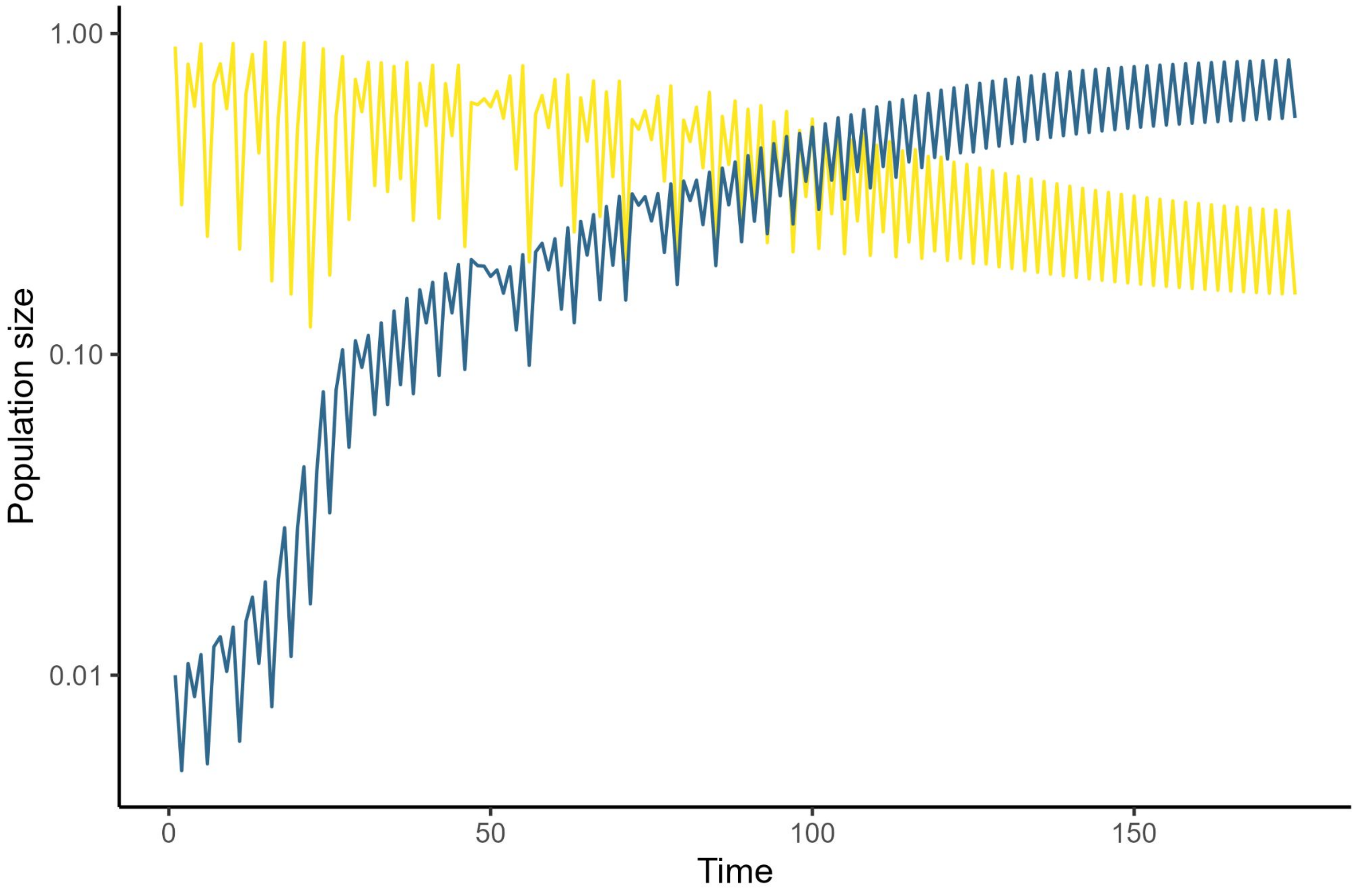
1.00
0.10
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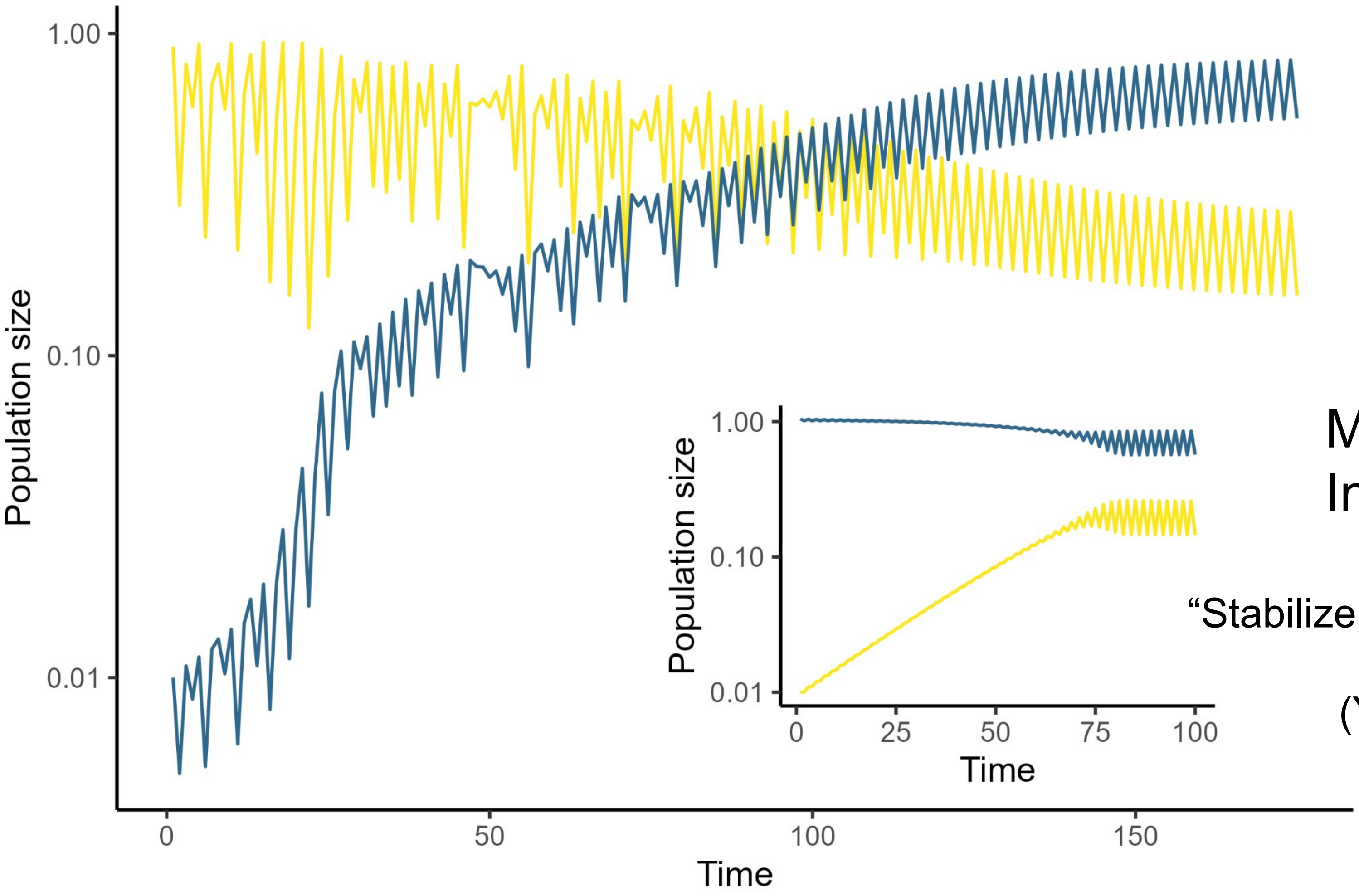
Time




# Mutual Invasibility

"Stabilizer-destabilizer trade-off" (Yamamichi & Letten 2022)

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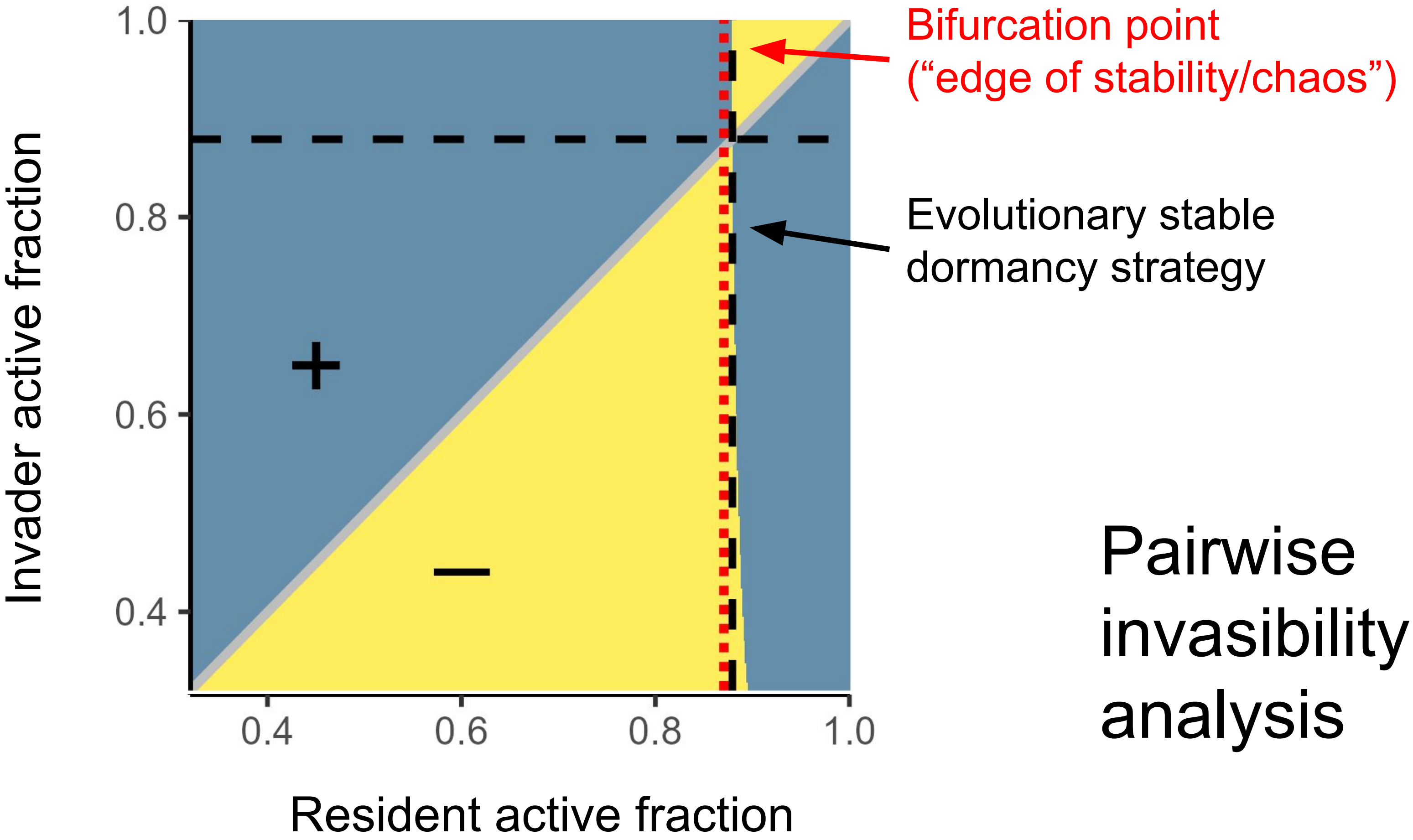


Pairwise invasibility analysis

## Extrinsic variability

- Temperature
- Precipitation
- Resource pulses
- …

## Intrinsic variability

Overcompensation in discrete time population dynamics
(pre-print online now)

**Multispecies interactions in continuous time
(work in progress)**

# Multiple species, continuous time

$$\frac{dn_i}{dt} = f_i(\mathbf{n})n_i - \alpha_i n_i + \beta_i q_i$$

$$\frac{dq_i}{dt} = \alpha_i n_i - \beta_i q_i - m q_i \qquad i = 1, 2, \ldots, S$$

# Multiple species, continuous time

**Resident community (fluctuating)**

$$\frac{dn_i}{dt} = f_i(\mathbf{n})n_i \quad i = 1, 2, \ldots, S$$

**"Mutant" species j with dormancy**

$$\frac{dn_{j'}}{dt} = f_j(\mathbf{n})n_{j'} - \alpha n_{j'} + \beta q_{j'}$$

$$\frac{dq_{j'}}{dt} = \alpha n_{j'} - \beta q_{j'} - m q_{j'}$$

# Dormancy advantage

- In the limit $m \to 0$, dormancy can always invade fluctuating resident dynamics
- This is a special case of dispersal-induced growth (DIG)!
- Interesting limiting cases: $\alpha, \beta >> 0$ (dormant fraction tracks growth rate) and $\alpha, \beta \approx 0$ (time-averaging)

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# Fast dormancy dynamics

- Change variables: $N(t) = n(t) + q(t)$ (total population) and $R(t) = n(t) / N(t)$ (active fraction)
- Define $\varepsilon = 1 / \beta$ and $\gamma = \alpha / \beta$ = constant

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- As ε → 0, the dynamics of active *R* are fast – we can take *R* to be at quasi-equilibrium:

$$R(f) = \frac{\sqrt{(1+\gamma-\epsilon f)^2+4\epsilon f}-(1+\gamma-\epsilon f)}{2\epsilon f}$$

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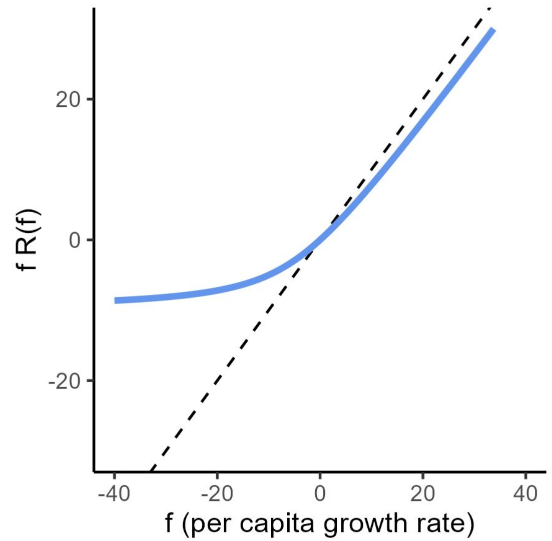
Realized per capita growth rate is convex in *f*



# Can dormancy stabilize community dynamics?

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# Can dormancy stabilize community dynamics?

- (Hadeler 2008): In general, dormancy can **stabilize or destabilize** dynamics
- If $\alpha_i = \alpha$, $\beta_i = \beta$ for all $i$, dormancy stabilizes
    - If $u \pm iv$, is an eigenvalue of the community matrix *without dormancy* and $u > 0$, then the corresponding eigenvalues *with dormancy* have negative real part iff

      $v^2 > 4\, u\, \alpha - (\alpha + \beta - u)^2$ and $v\, (\beta - u) > u\, (\alpha + \beta - u)^2$

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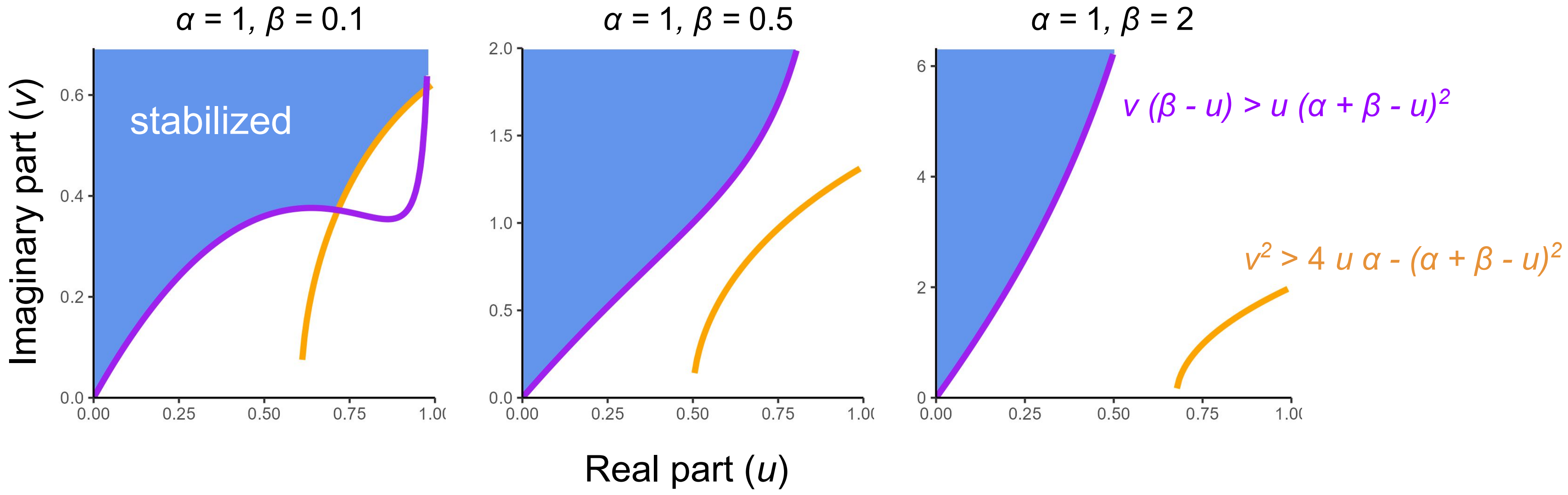

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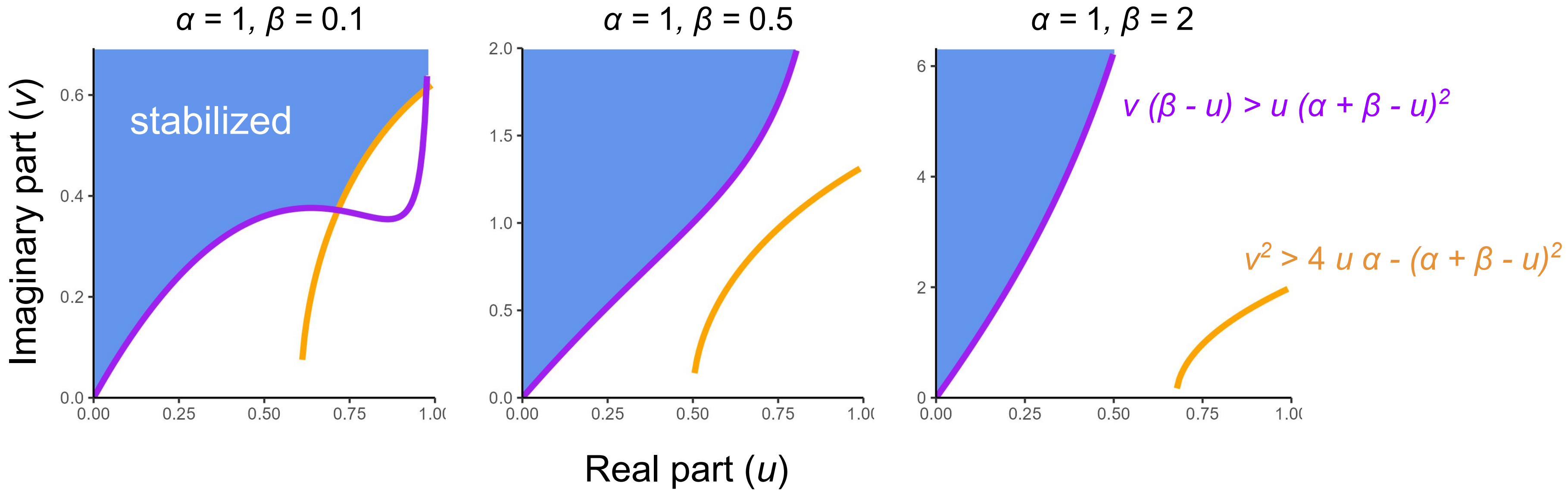
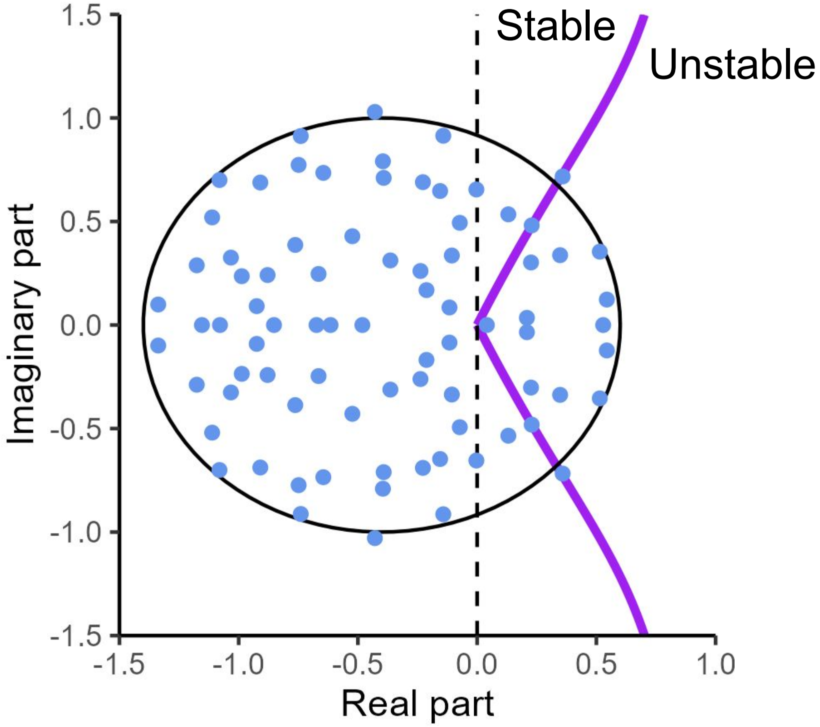



Stabilization requires $\alpha > u$ and $v$ large compared to $u$

# Which dynamics can dormancy stabilize?

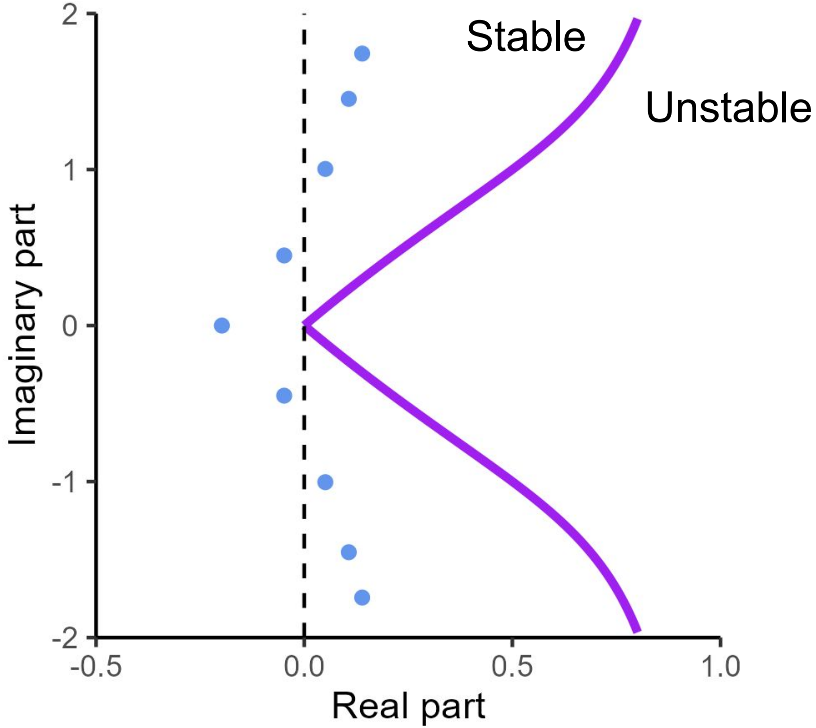


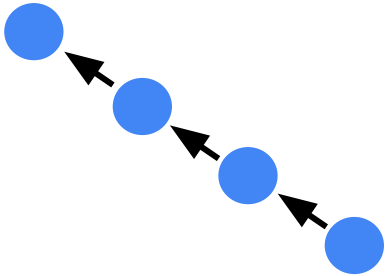

Interaction matrices described by elliptic ensembles **cannot** generally be stabilized by dormancy

# Which dynamics can dormancy stabilize?

- Dormancy can stabilize against Hopf bifurcations
  - Associated with food chain/web dynamics
- Bilinsky and Hadeler (2009) showed that dormancy can stabilize MacArthur-Rosenzweig predator-prey dynamics

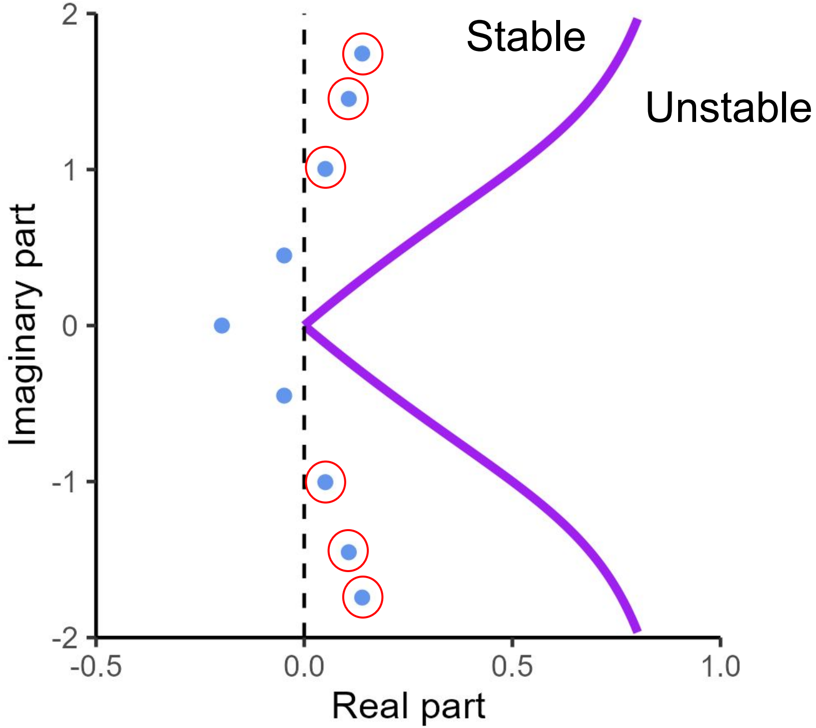
# Linear food chain

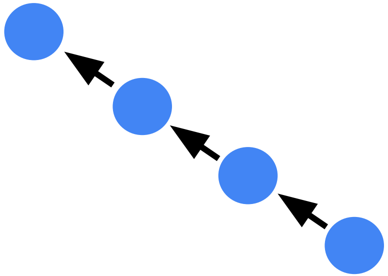


Generic food chain model (after Gross et al. 2005) exhibits chaotic dynamics that can be stabilized by dormancy

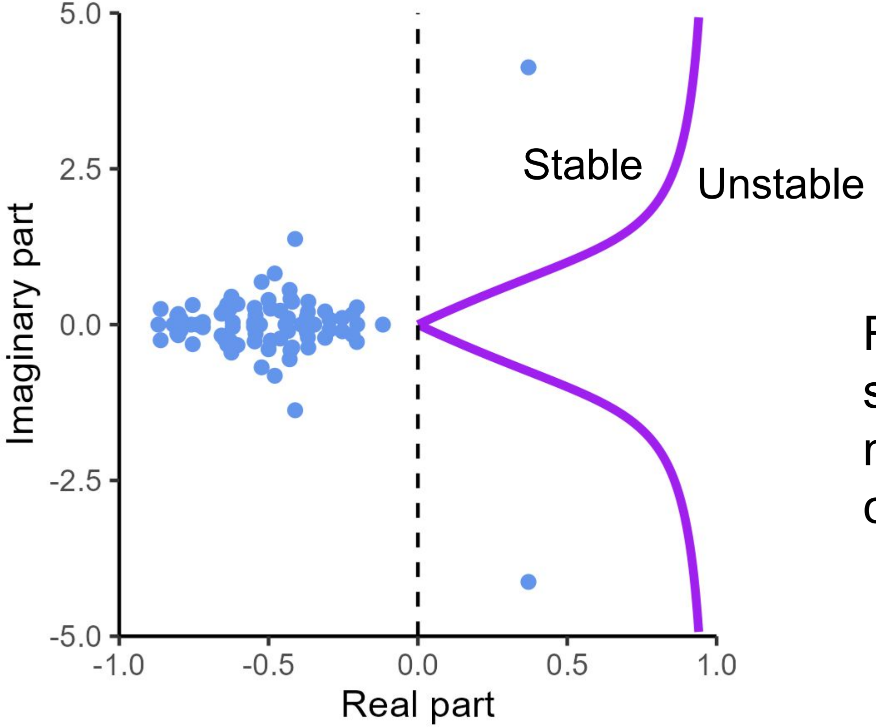
# Linear food chain

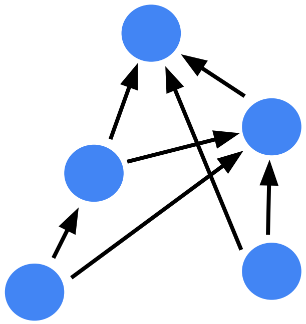


Generic food chain model (after Gross et al. 2005) exhibits chaotic dynamics that can be stabilized by dormancy

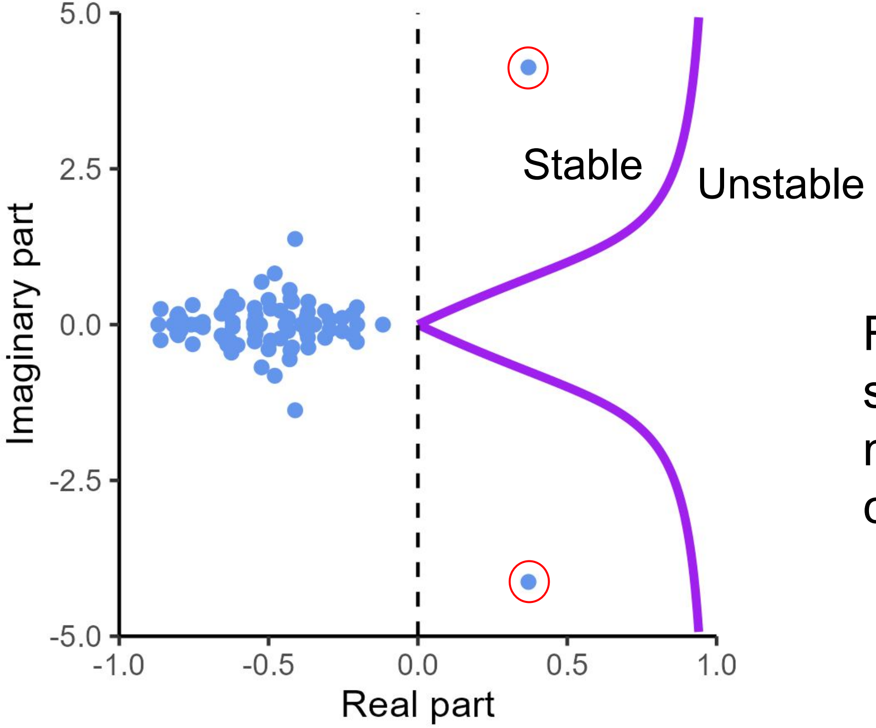
# Random food web

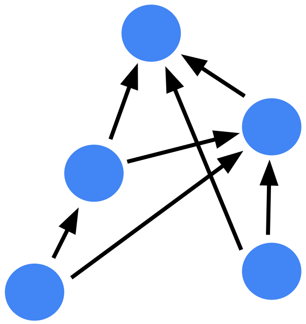


Random food webs with hierarchical structure (after Allesina et al. 2015) may have outlying eigenvalues that can be stabilized by dormancy

# Random food web



Random food webs with hierarchical structure (after Allesina et al. 2015) may have outlying eigenvalues that can be stabilized by dormancy

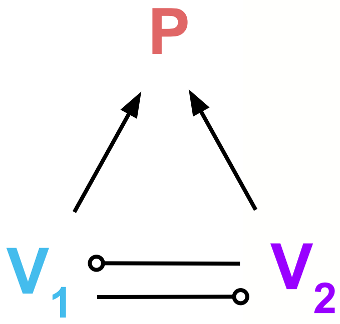
# Evolution of dormancy in a single species

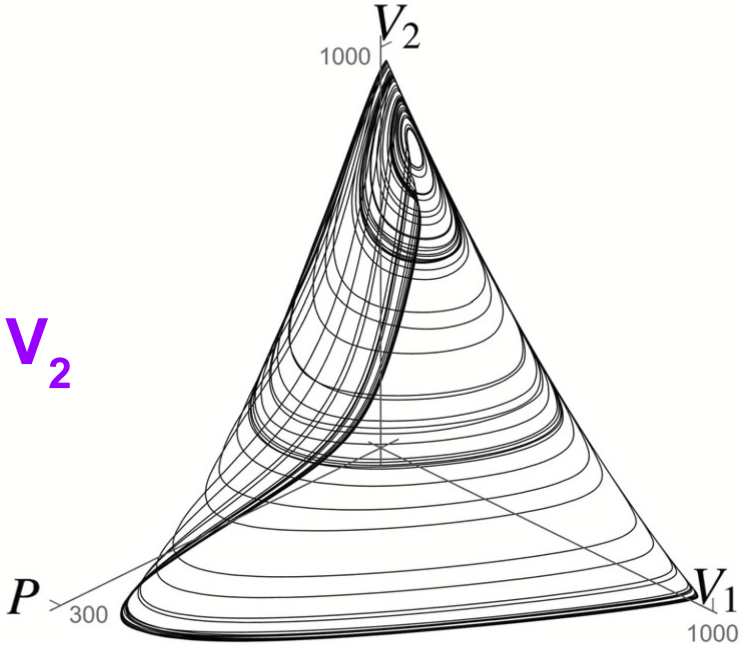
- Hadeler’s analysis applies to systems with highly symmetric dormancy
- In general, determining stabilization by dormancy is hard
- We are most interested in cases where dormancy evolves in one species
- **Open question: Can we characterize this case?**

# Evolution of dormancy in a single species

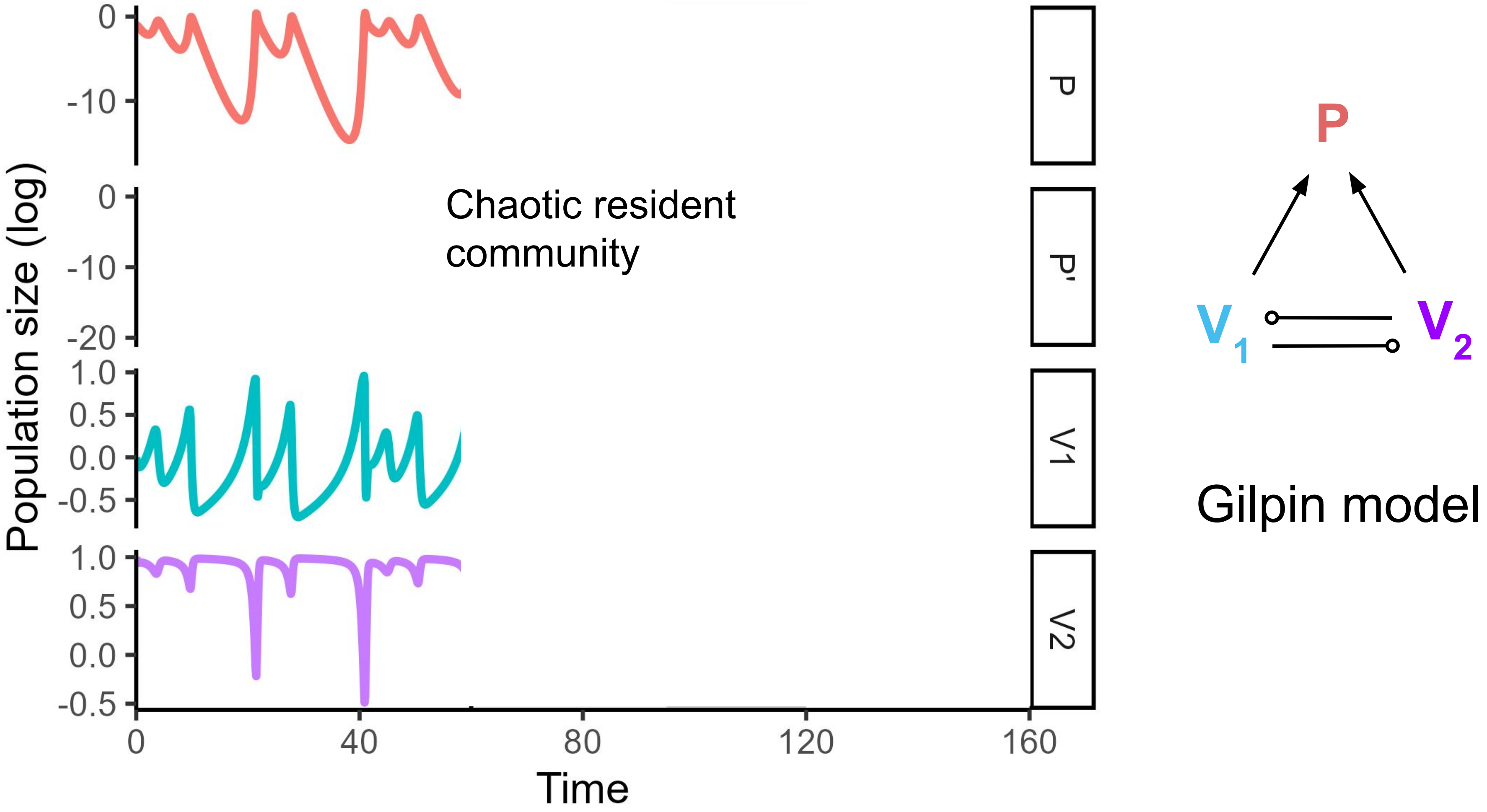
Simple food web model (Gilpin 1979):

- One predator (P)
- Two competing prey ($V_1$ and $V_2$)
- Lotka-Volterra dynamics

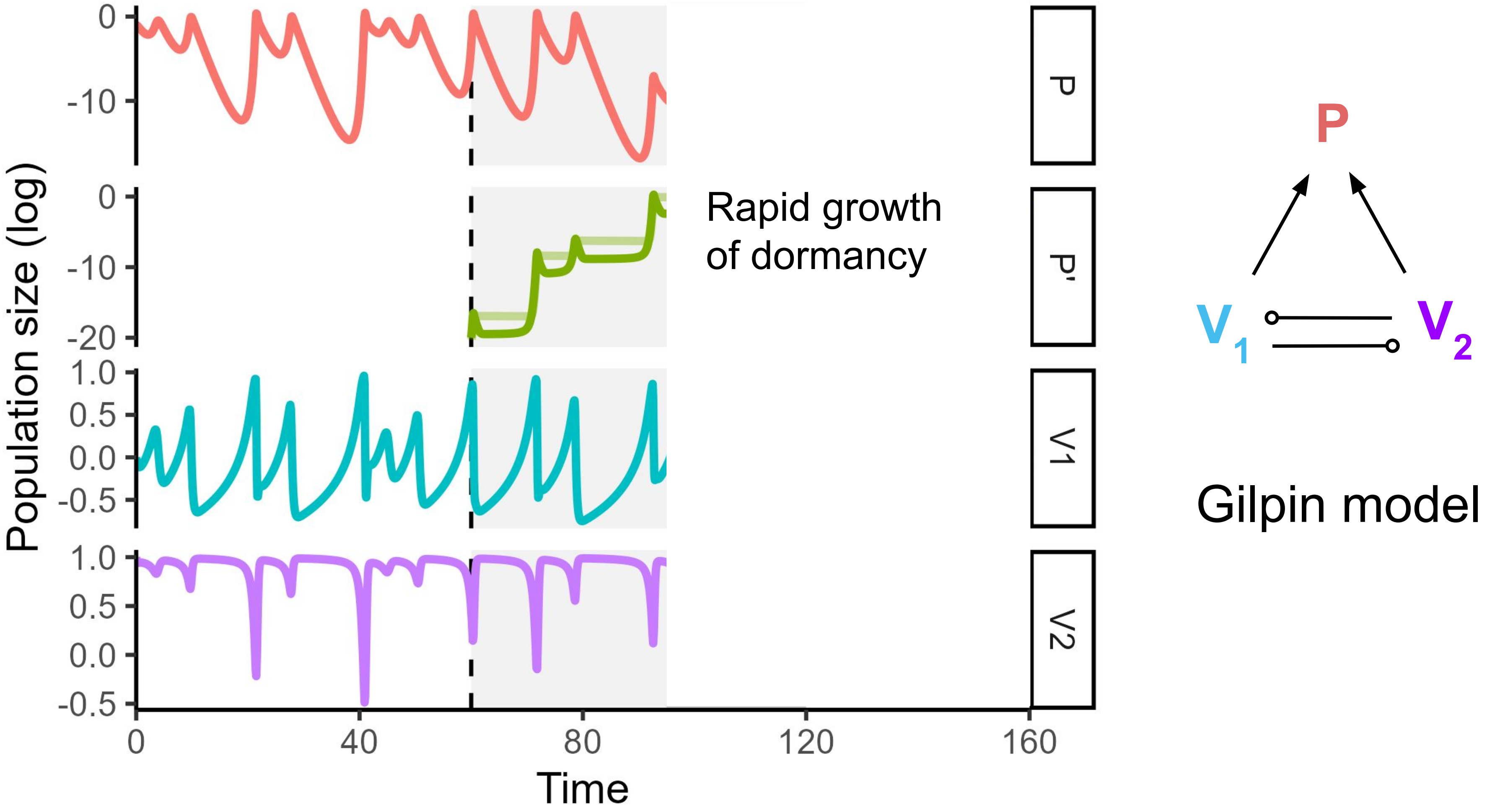


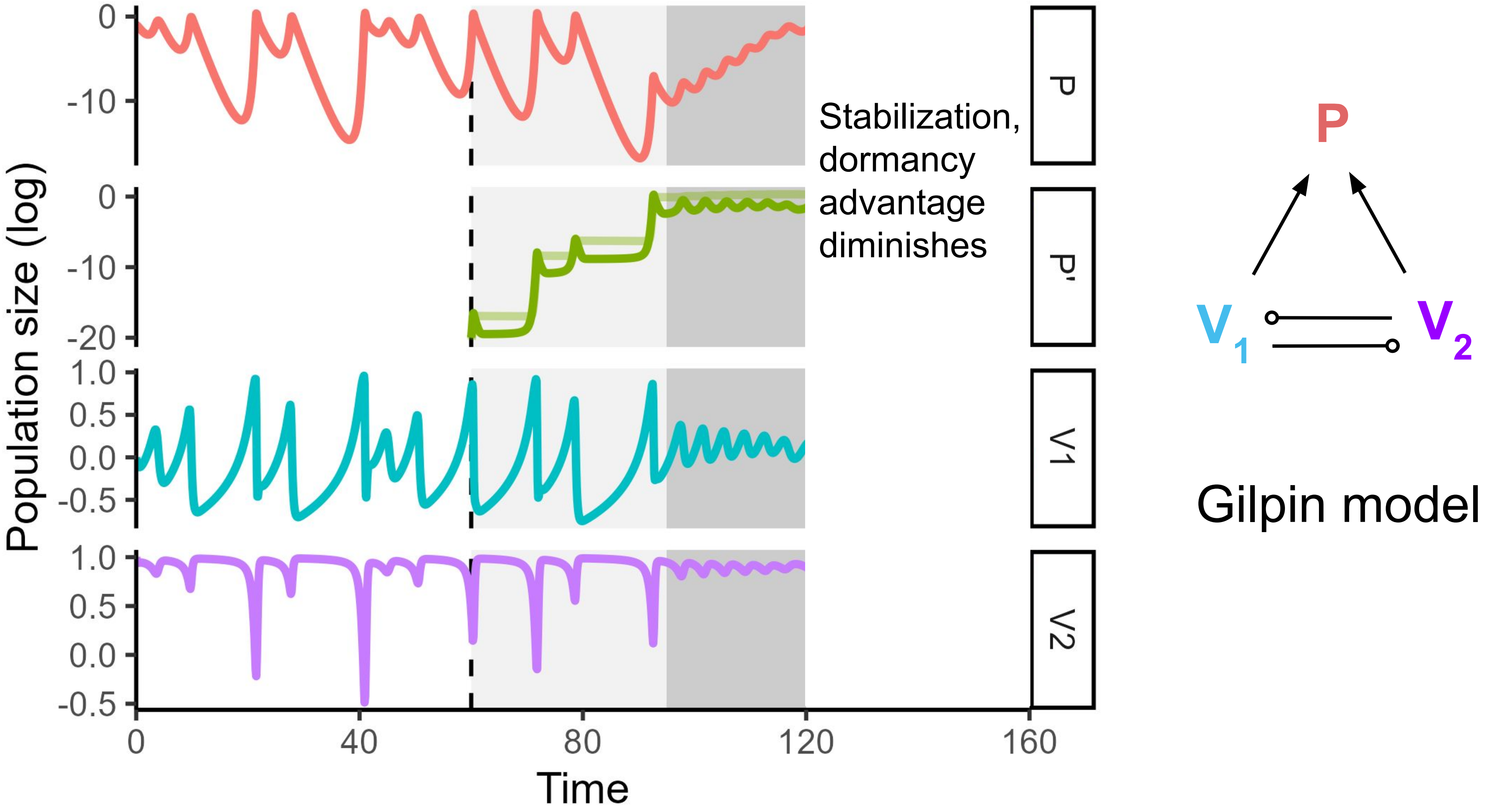

Robey et al. (2024)



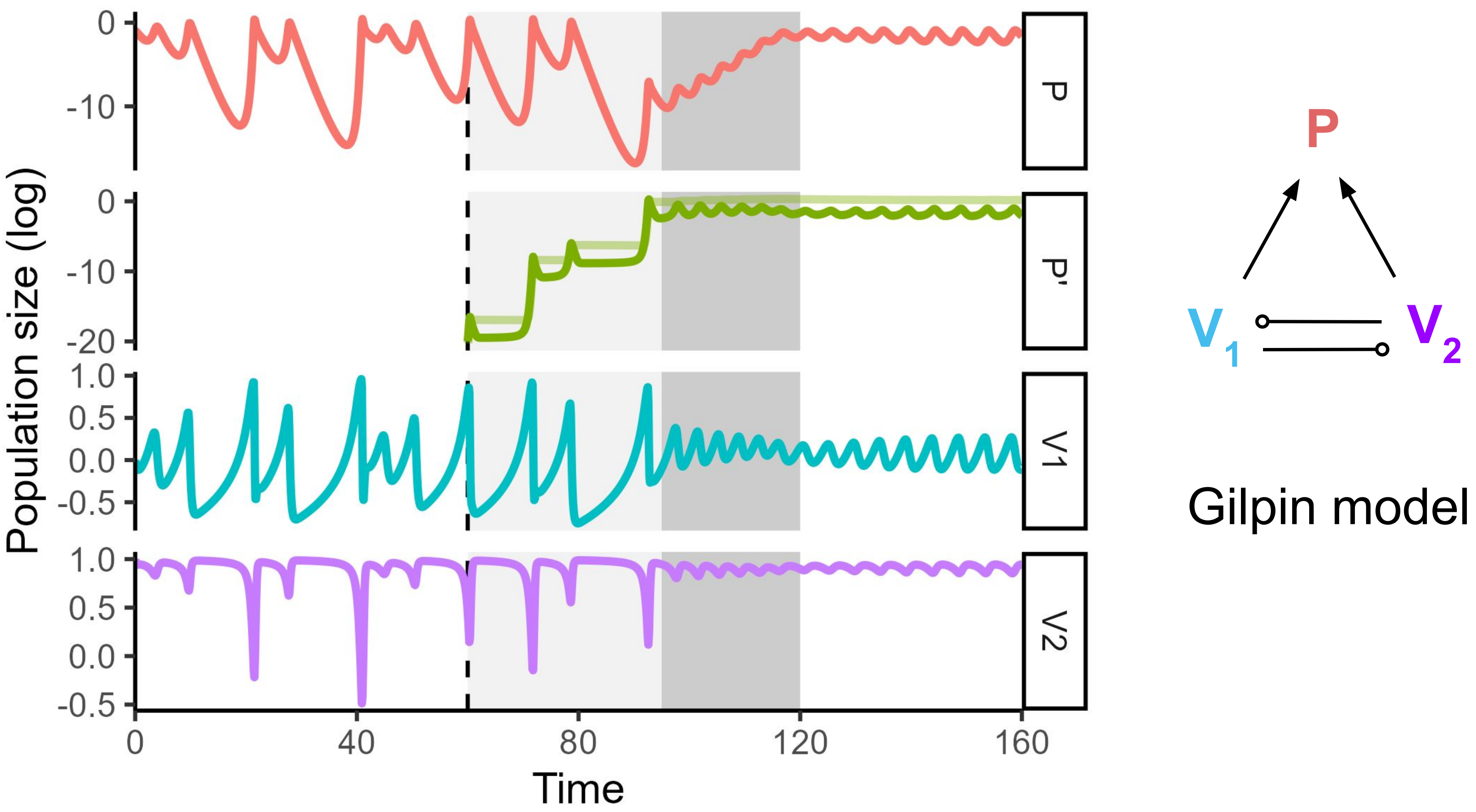
Population size (log)
0
-10
P
0
-10
-20
P'
Chaotic resident community
1.0
0.5
0.0
-0.5
V1
1.0
0.5
0.0
-0.5
V2
0
40
80
120
160
Time
P
V1
V2
Gilpin model



Population size (log)
0
-10
-20
1.0
0.5
0.0
-0.5
P
P'
V1
V2
Rapid growth
of dormancy
0
40
80
120
160
Time
P
$V_1$
$V_2$
Gilpin model



Population size (log)
0
-10
-20
1.0
0.5
0.0
-0.5
0
40
80
120
160
Time
Stabilization,
dormancy
advantage
diminishes
P
P'
V1
V2
P
V1
V2
Gilpin model



Population size (log)
0
-10
P
0
-10
-20
P'
1.0
0.5
0.0
-0.5
V1
1.0
0.5
0.0
-0.5
V2
0
40
80
120
160
Time
P
$V_1$
$V_2$
Gilpin model

# Some conclusions

- Fluctuating dynamics should be vulnerable to **invasion and suppression** by dormancy
- Trade-offs between dormancy strategies can enable **coexistence**
- Evolution of dormancy may drive dynamics to the "**edge of stability**"
- In **multispecies communities**, fluctuating dynamics favor evolution of dormancy, but dormancy is only sometimes stabilizing
  - Dormancy stabilizes **trophic dynamics**
  - Rich, open questions related to **interaction of dormancy with network structure**

# Thanks for listening!

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Pincelli Hull

Thanks to Hull and Vasseur labs for discussions

Schmidt Sciences

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**Stabilization of fluctuating population dynamics via the evolution of dormancy**

Zachary R. Miller, David Vasseur, Pincelli M. Hull

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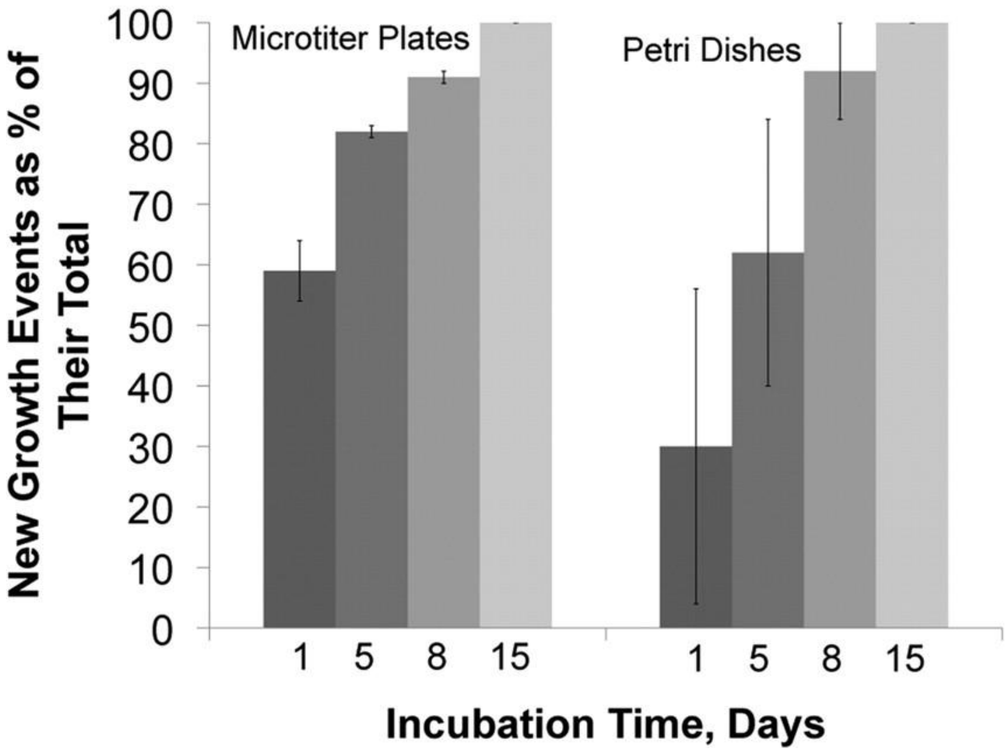
# Dormancy as a bet-hedging strategy




**Stochastic dormancy kinetics**

Buerger et al. (2012)
App. and Env. Microbio.