



Evolution of Ecological Communities

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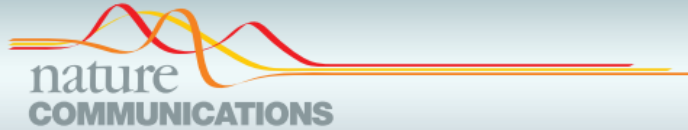


Interlocking timescales

- Celiker *et al.*
 - or: how ecology affects evolution
- Braakman *et al.*
 - or: how evolution affects ecology
- Vetsigian
 - or: how interlocking timescales effect even more emergent patterns

Celiker *et al.*

- How ecology affects evolution
- Wet lab
- 6-species bacterial ecosystem evolution
- 96 parallel replicates, ~400 generations



ARTICLE

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Clustering in community structure across replicate ecosystems following a long-term bacterial evolution experiment

Hasan Celiker¹ & Jeff Gore²

Experiments to date probing adaptive evolution have predominantly focused on studying a single species or a pair of species in isolation. In nature, on the other hand, species evolve within complex communities, interacting and competing with many other species. It is unclear how reproducible or predictable adaptive evolution is within the context of a multi-species ecosystem. To explore this problem, we let 96 replicates of a multispecies laboratory bacterial ecosystem evolve in parallel for hundreds of generations. Here we find that relative abundances of individual species vary greatly across the evolved ecosystems and that the final profile of species frequencies within replicates clusters into several distinct types, as opposed to being randomly dispersed across the frequency space or converging fully. Our results suggest that community structure evolution has a tendency to follow one of only a few distinct paths.



Methods (1) (Celiker *et al.*)

- 6 Bacterial species
 - No aggressive antagonization (e.g. no predation)
 - Partially overlapping carbon utilization profiles
- Ancestral communities
- Isolated evolution
 - Strains evolved in isolation for ~400 generations, then mixed on agar
- Multispecies evolution
 - Strains mixed and plated together for ~400 generations

Methods (2) (Celiker *et al.*)

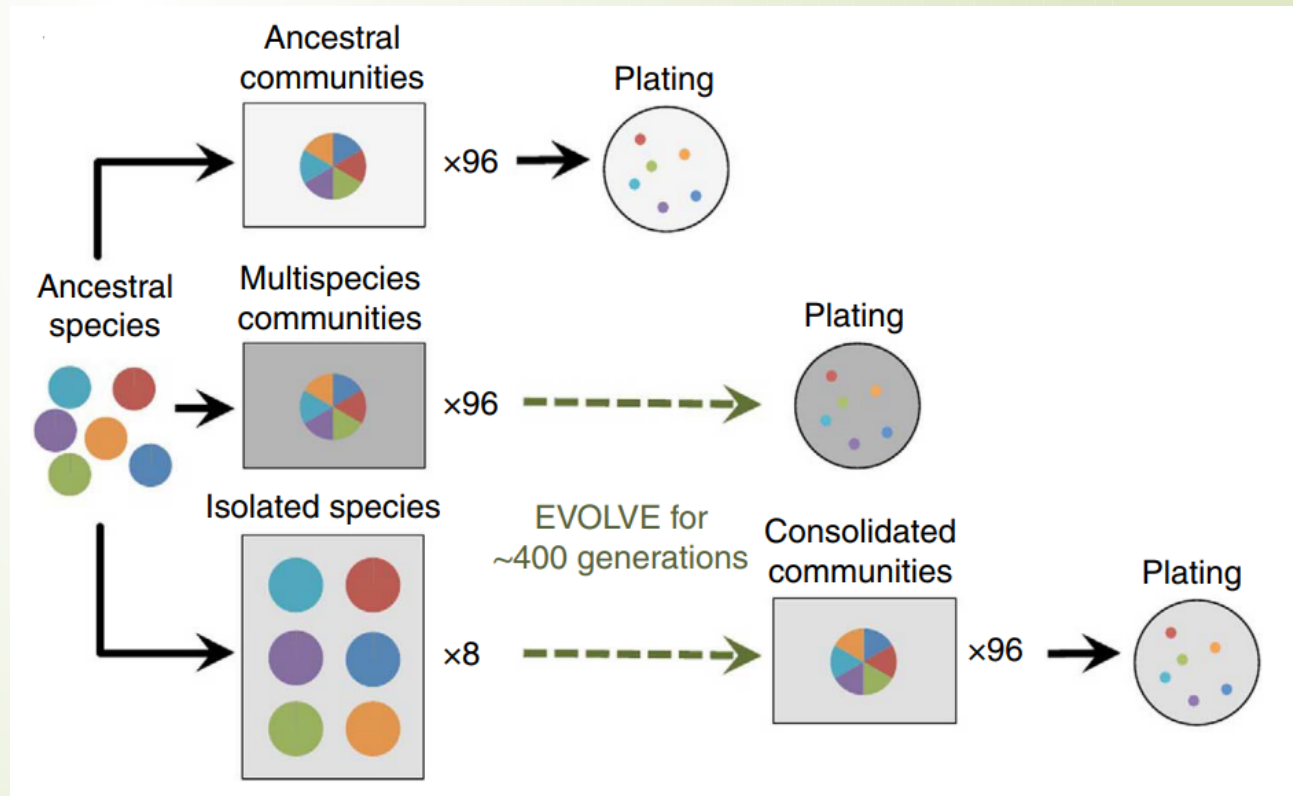


Fig 2. Evolution experiment design.

Results (1) (Celiker *et al.*)

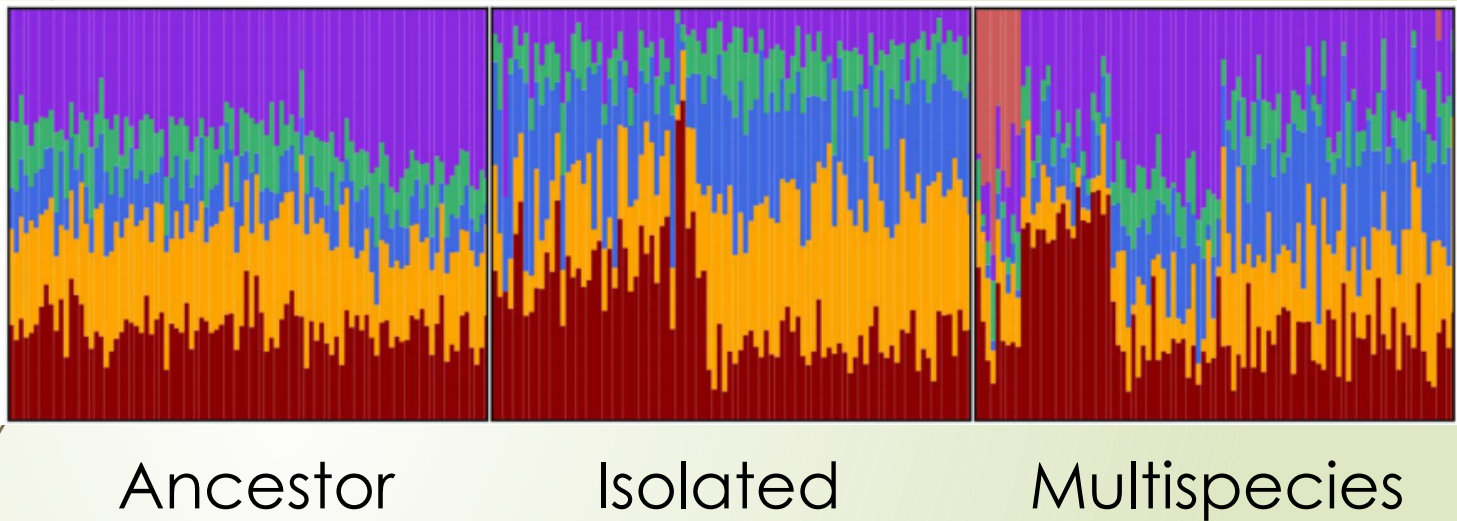


Fig. 3 clustered stacked area plots of raw relative abundance

Results (2) (Celiker *et al.*)

- Results were clustered in k clusters
- k with the highest Calinski-Harabasz index was selected
- i.e. the highest inter-to intracluster variation.
- $K=4$ for mixed evo
- $K=2$ for isolation

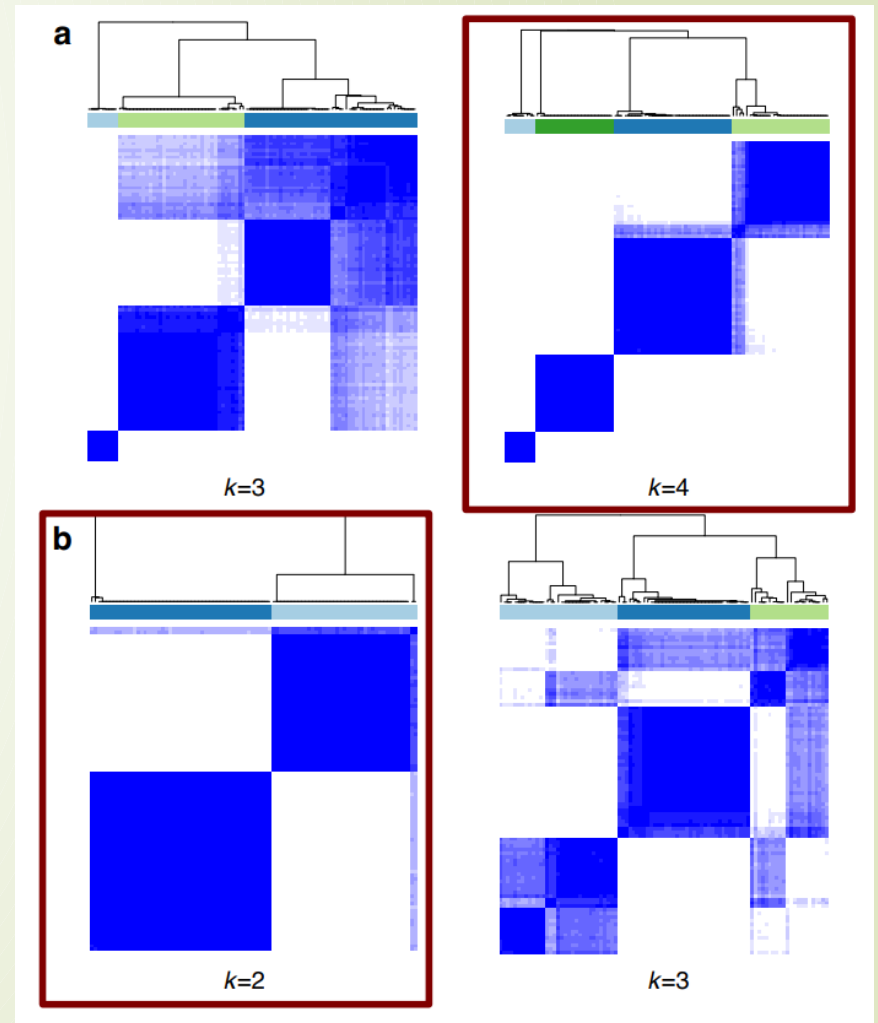


Fig. 4 consensus clustering results (trimmed)

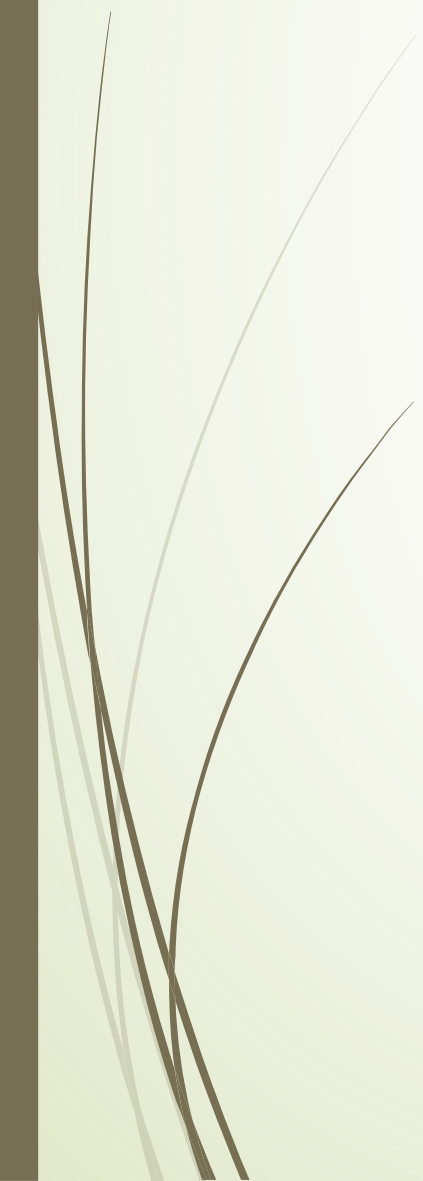


Results (3) (Celiker *et al.*)

- Only limited evolutionary pathways
- Available pathways are shaped by ecology
- Clusters are the result of dominance of driver species
 - Single species discovers a competitively advantageous mutation, changing the ecological landscape
- *Pseudomonas putida* (PP) abundance fell to negligible levels in ancestral and isolated communities
 - In one cluster of mixed evo, PP became dominant driver species instead



Discussion (*Celiker et al.*)

- Experiment might have been too short
 - “Unique” clusters might converge to single point over longer timescales
 - Compare “Virtual Microbe” experiments
 - Sometimes an alternative trajectory is just an alternative trajectory
- 

Braakman
et al.

- How evolution affects ecology
- Reconstruction of *Prochlorococcus* marine cyanobacterium metabolism
- Metabolism can create new ecological niches
- Emergent mutualism

PNAS

Metabolic evolution and the self-organization of ecosystems

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Contributed by Sallie W. Chisholm, February 22, 2017 (sent for review November 28, 2016; reviewed by Ron Milo and John A. Raven)



Methods (1)

(Braakman *et al.*)

- Prochlorococcus strains exist phylogenetically ordered in vertical ocean strata
 - Newer clades are in high-sunlight, low-nutrient upper strata
- Changes to the metabolic core of Prochlorococcus were reconstructed

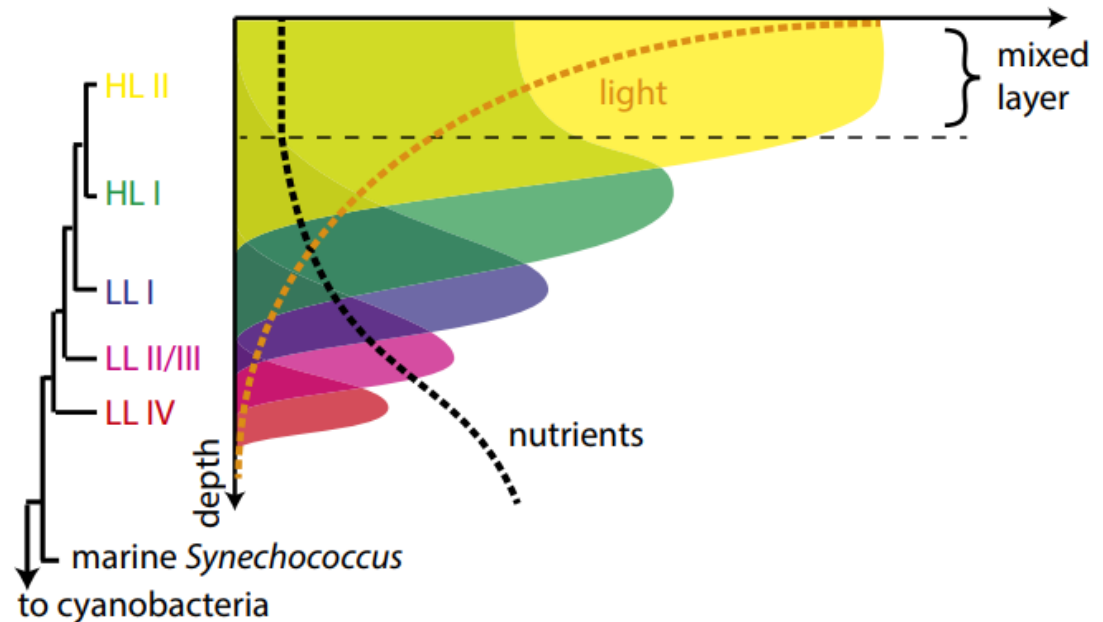



Fig. 1 typical relative abundance distribution of *Prochlorococcus* ecotypes and resources



Methods (2) (Braakman *et al.*)

- ▶ High Light Prochlorococcus has higher photosynthetic capacity, but leaks organic carbon compounds
 - ▶ Carbon compounds as redox outlet?
- ▶ Public goods dilemma?
 - ▶ Why not just reduce electron flux capacity instead?
- ▶ Expression assay shows malate uptake pathway activates at night
 - ▶ Potential mutualism?

Results (1) (Braakman *et al.*)

- Newer strains have higher electron flux density v_e
 - More photodamage repair mechanisms
- Newer strains also have lower nutrient flux density v_n
 - By decreasing growth rate
 - By decreasing N and P usage of the genome
 - By decreasing N-rich amino acid use
 - By swapping P-lipid to sulfolipid membranes
 - By decreasing Fe use in photosynthetic machinery
- Summarized: v_e/v_n increases as new strains

Results (2) (Braakman et al.)

$$[n] = \frac{K_{M,n}}{[E]k^+} \frac{\nu_n}{1 - e^{\Delta_r G/RT}} = \frac{K_{M,n}}{[E]k^+} \frac{Q_n}{Q_C} \frac{\nu_e(\#C/\#e)(1 - \beta)}{1 - e^{\Delta_r G/RT}}.$$

- Plugging in simplified Michaelis-Menten kinetics (above) under strong nutrient limitation:
 - High ν_e = high nutrient handling rate
 - Free energy costs for nutrient uptake can become very large iff the inside-outside gradient is not reduced
 - Mechanisms exist for ATP/ADP ratios to decrease this gradient
 - Ex. High ATP/ADP ratios mean low internal P_i concentrations, reducing the P-gradient
 - Similar mechanisms for N

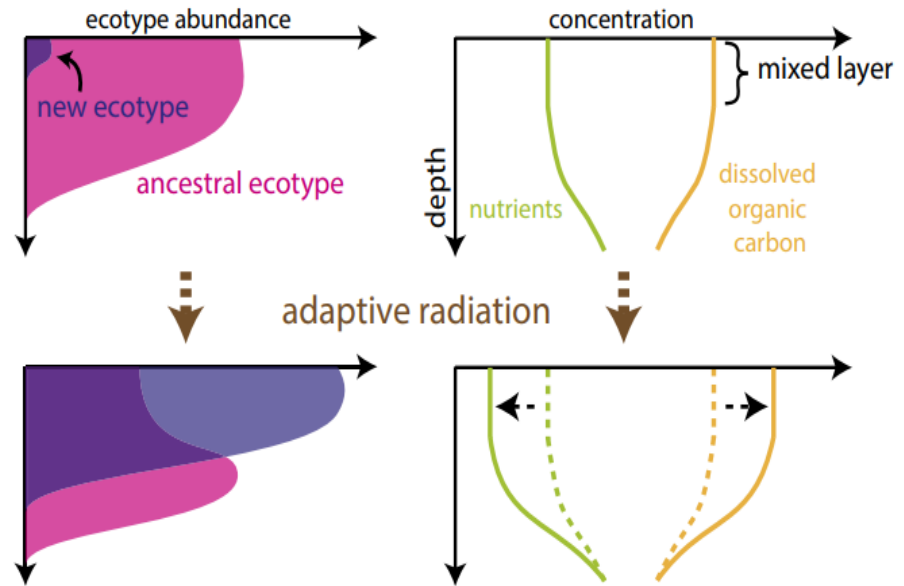
Results (3) (Braakman *et al.*)


- Aforementioned kinetics can be used to calculate $[n]$, which is the minimal nutrient density for density-negative growth. ~~helps lower v_e/v_n~~ helps lower $[n]^*$
- However, to avoid ADP-limitation, ATP use must be increased to help handle increased metabolic load
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 - Carbon is a good sink
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 - BUT: growth limited, and high v_e/v_n strains have low growth
 - Solution: dump organic carbon
- Solution: dump organic carbon

Results (4) (Braakman *et al.*)

Ecological effects
of evolution:


- New nutrient efficient ecotypes decrease nutrients in higher strata, and push older ecotypes down
- Free organic carbon is a good opportunity for heterotrophs
 - Low efficiency, high metabolic rate





Discussion (1) (Braakman *et al.*)

- Emerging mutualism
 - Heterotrophs that feed Prochlorococcus have an advantage: SAR11 might feed malate
 - Prochlorococcus depends on heterotrophs to detoxify the H₂O₂ its photosystems create
- Parallels to plant evolution
 - coccus is the chloroplast, SAR11 the mitochondrion, other heterotrophs (SAR86, SAR116?) the liposome
- “Black queen” dynamics: evolutionary race that pulls everyone towards higher total biomass



Discussion (2) (Braakman *et al.*)

- Post-hoc explanation
 - Sensitive to human pre- and misconception
- “Reasonable” metabolic model
 - Feasibility needs to be verified

Vetsigian

- Eco-evo interplay
- Organisms create ecological niches
- Bacterial antibiotic production/resistance/degradation model shown stable, but is it evolutionarily reachable?

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Diverse modes of eco-evolutionary dynamics in communities of antibiotic-producing microorganisms

Kalin Vetsigian

Methods (1) (Vetsigian)

- Three phase life cycle:
 - Sporulation to random locations
 - Growth (homogenous speeds)
 - Resource competition

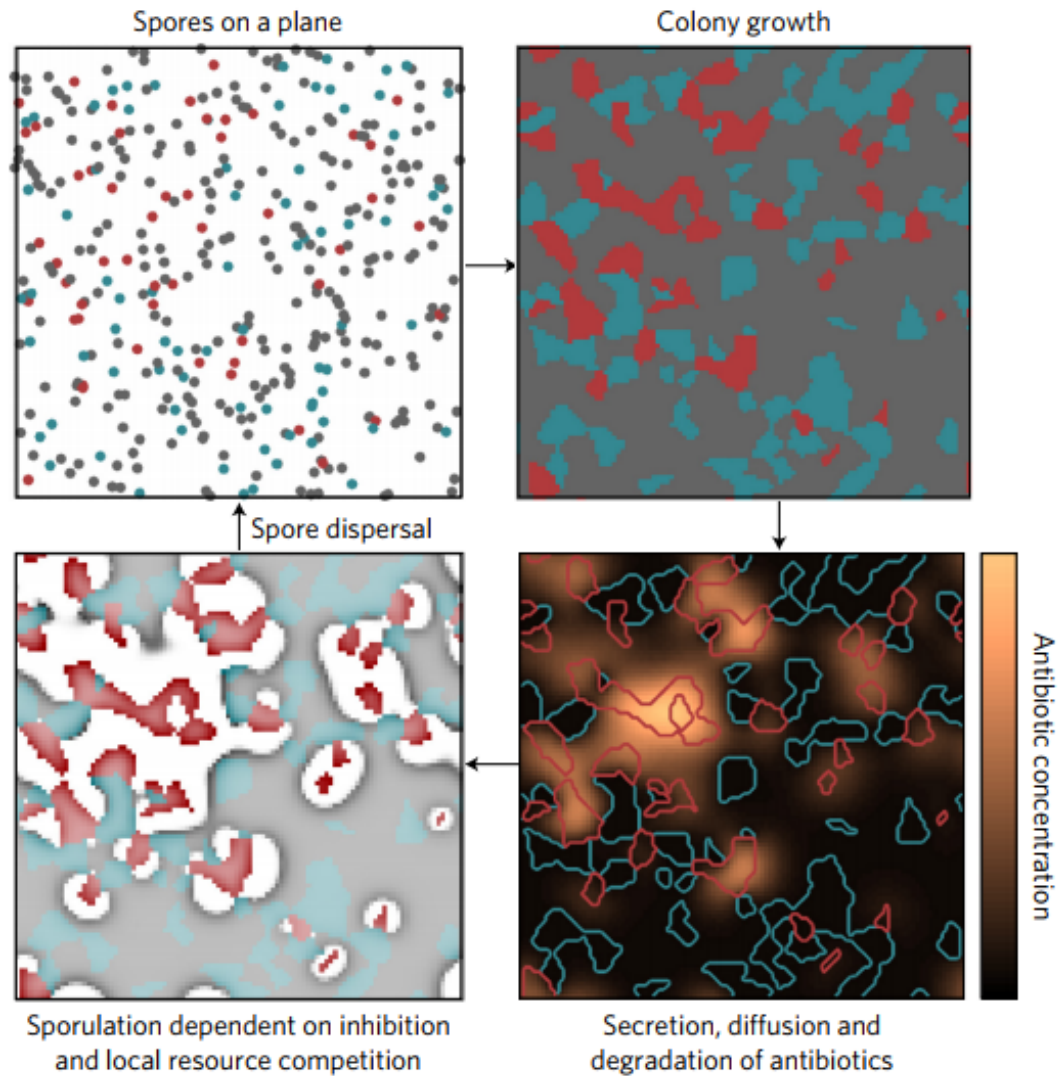



Fig. 1 Model overview



Methods (2) (Vetsigian)

- Bacteria have a one-dimensional affinity for antibiotics
 - (D) Degraders are resistant at constant + unit cost
 - (S) Sensitives are just that
 - (R) Resistant pay constant + unit cost for operation of an efflux pump
 - (P) Producers pay constant + unit cost for production and operation of an efflux pump
- Possible mutations were parameter size shifts (“point mutations”) as well as loss of function (any→S) and global (any→any) mutations



Results (1) (Vetsigian)

- For one dimensional experiment, evolutionary stable communities were all of the [D, S, P] motif
- Two-dimensional experiments had only combinations of this motif as evo stable communities [SS, SD, DS, PS, SP] [DD, SD, DS, PS, SP]
- Eco-evo patterns were explored, and most strikingly varied with Resistance/Efflux constant cost

Results (2) (Vetsigian)

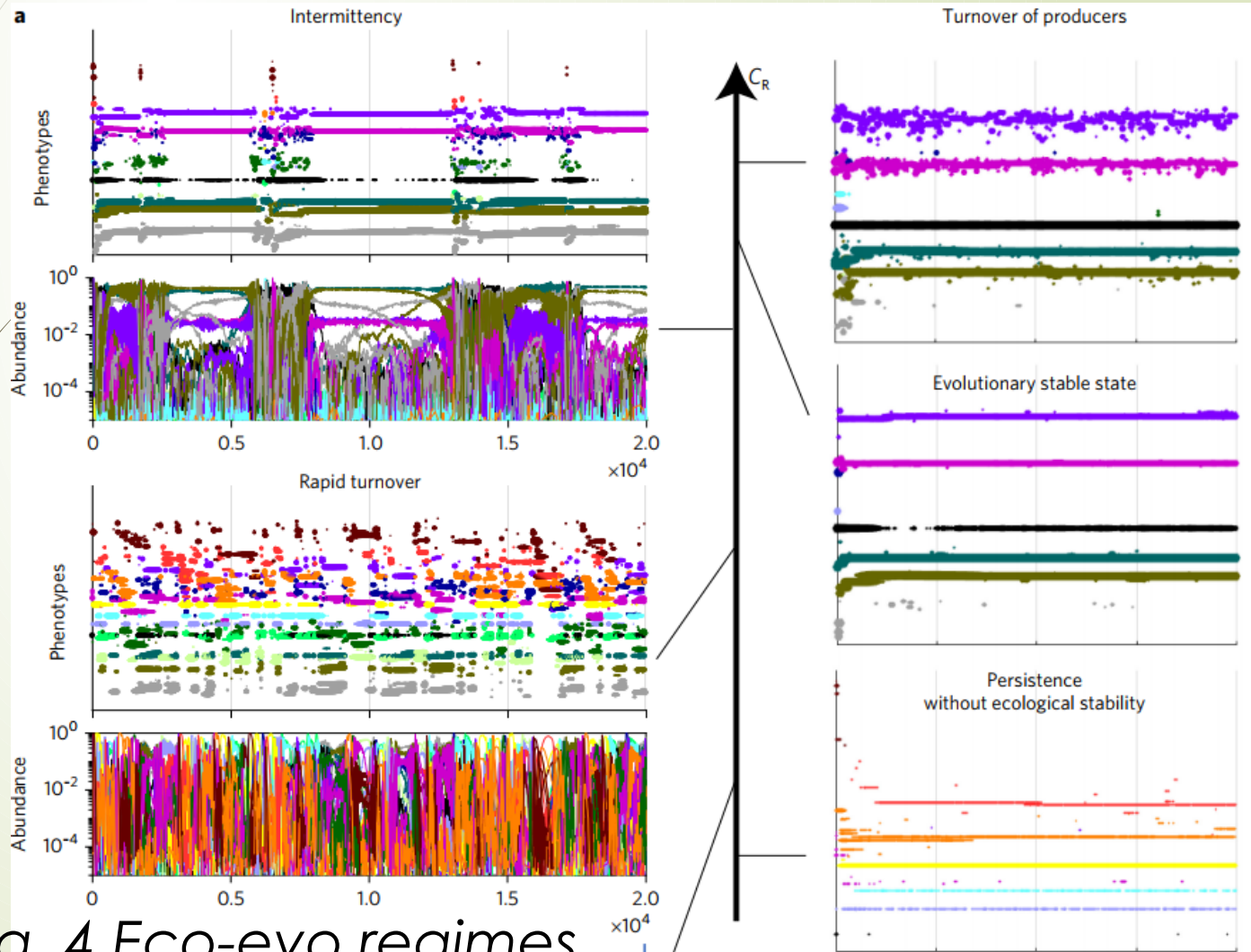


Fig. 4 Eco-evo regimes

Discussion (Vetsigian)

- Intermittent regimes might not need external destabilization, but might be an effect of eco-evo dynamics
- Low C_r regimes were eco-evo stable, but ecologically unstable
 - Only loss of function mutations required for stability

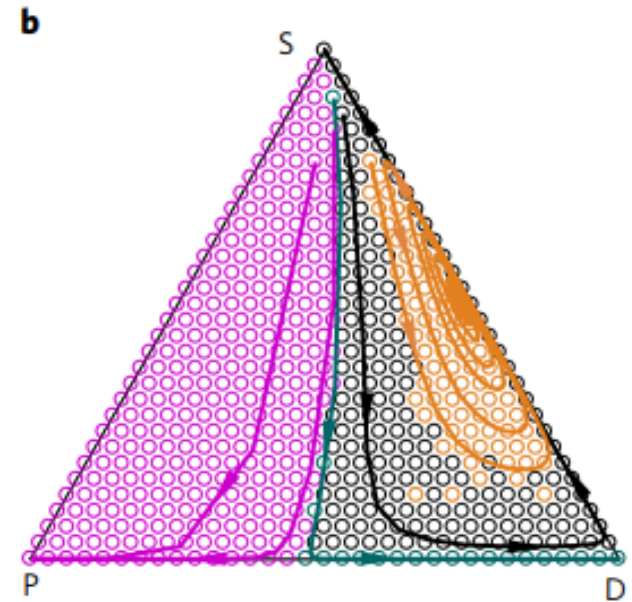



Fig. 2b phase portrait of ecological dynamics



Discussion (2) (Vetsigian)

- Consistent with earlier eco-evo simulations
 - Mutations needed for ecological stability
- Another example of speciation “without predefined ecological niches”