Survival Games: Planktonic Diversity Examined Through Non-Cooperative Game Theory

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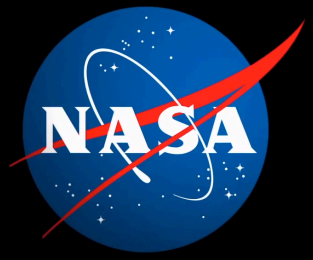
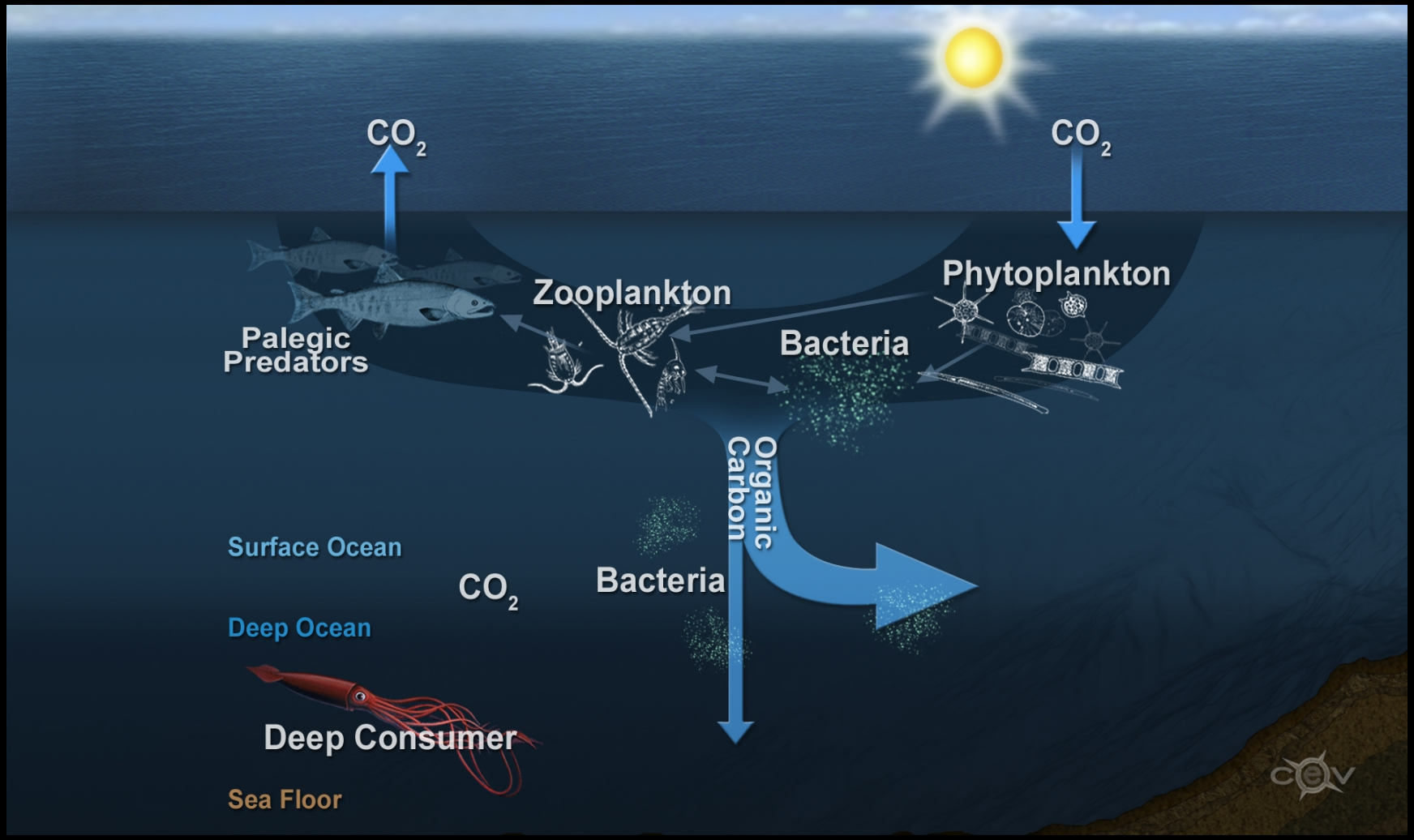
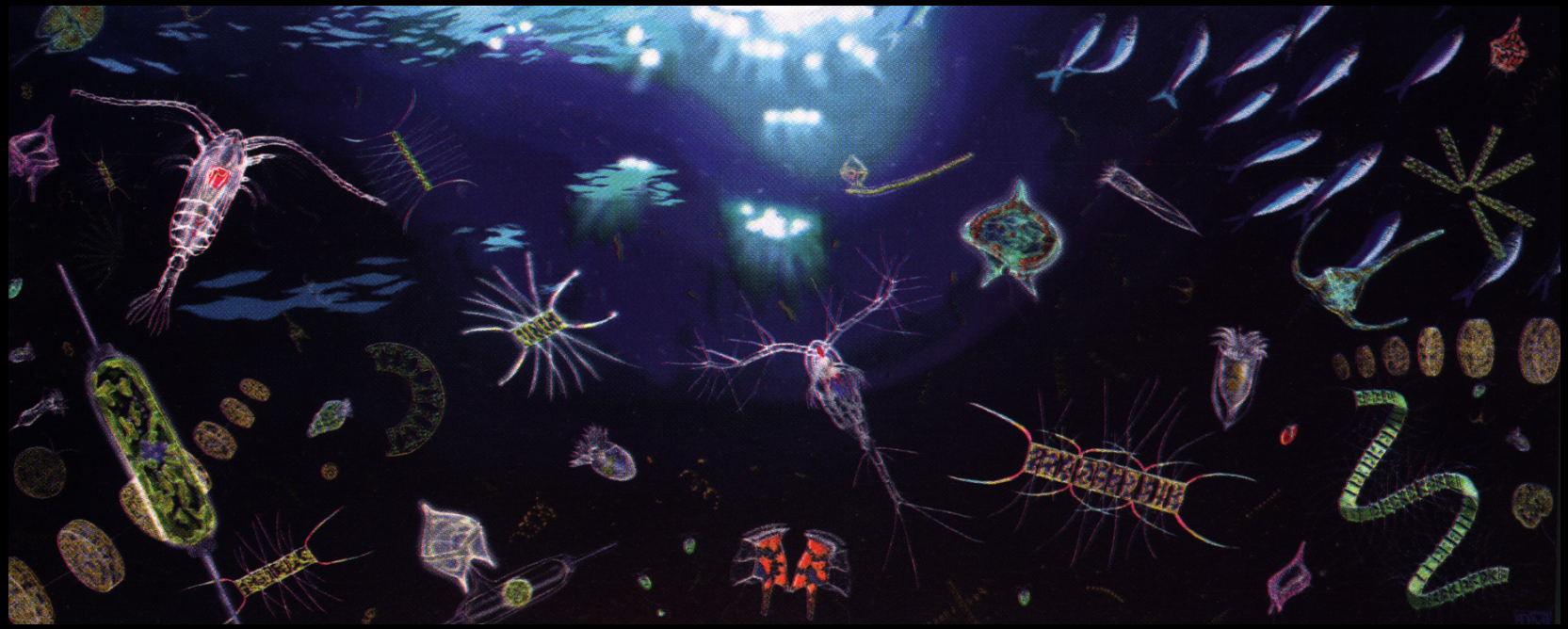




Paradox

Courtesy of John Delaney - with modifications



Paradox

2 Goals:

1. pervasive intra-specific trait variability in physiology, morphology and behavior in unicellular plankton

2. intra-specific variability alters population dynamics and is adaptive

Paradox

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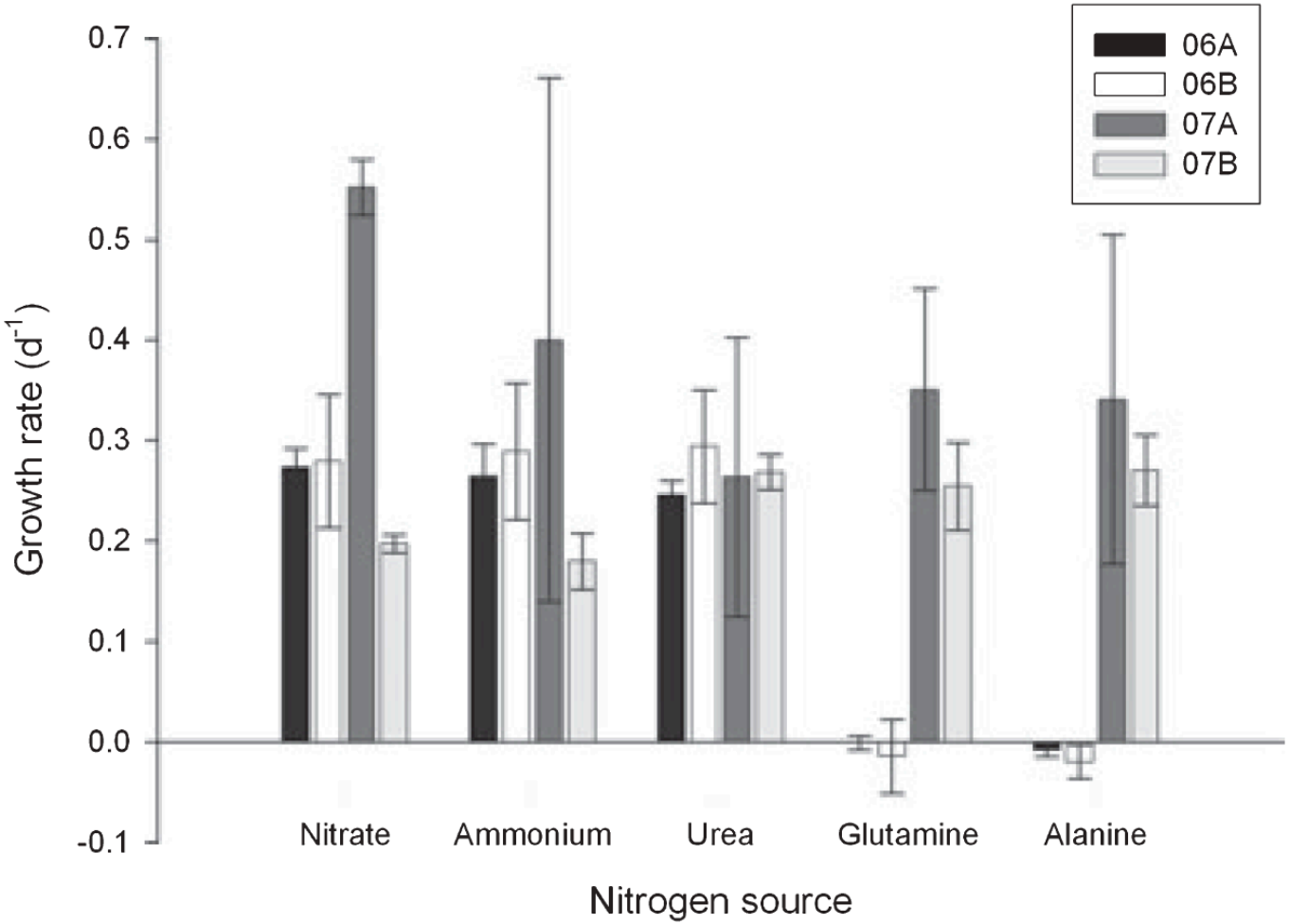
Pervasive intra-specific variability…

- growth rate variation as a function of nitrogen source for strains of phytoplankter *Heterosigma akashiwo*

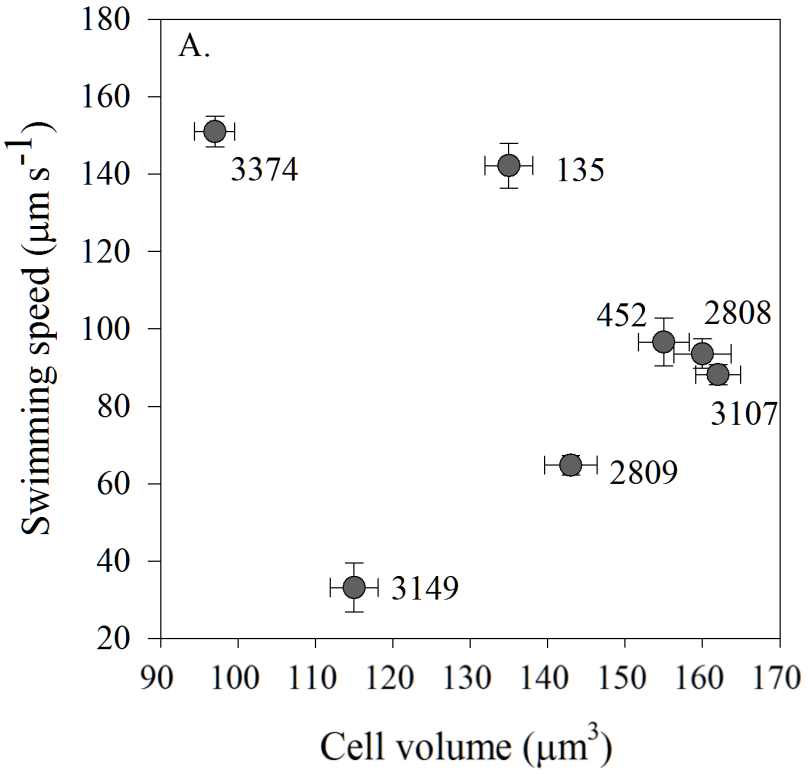


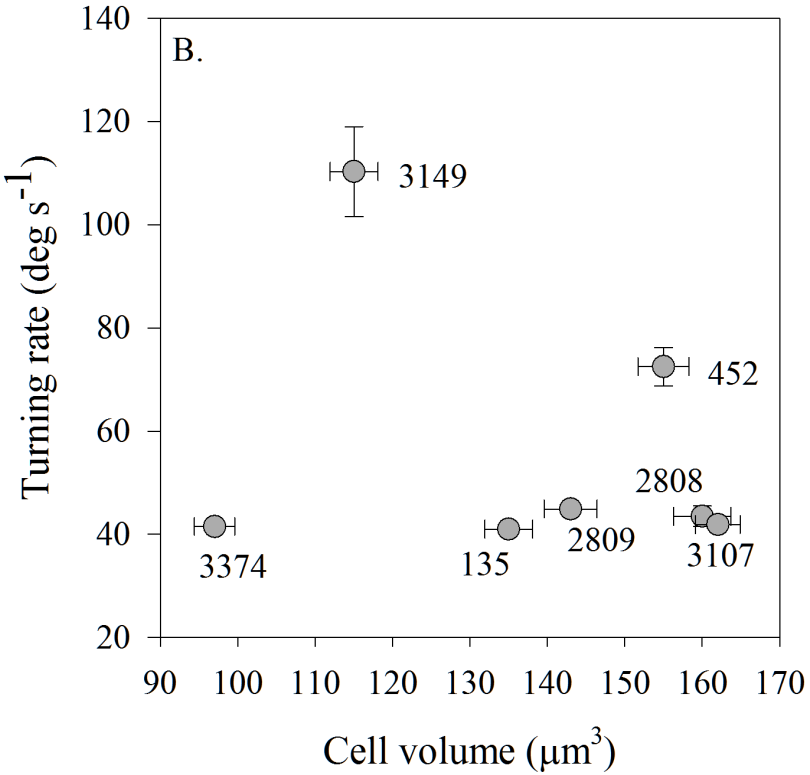
Paradox

Fredrickson et al 2011

Pervasive intra-specific variability…

- variable motility across strains of same phytoplankton species *Heterosigma akashiwo*



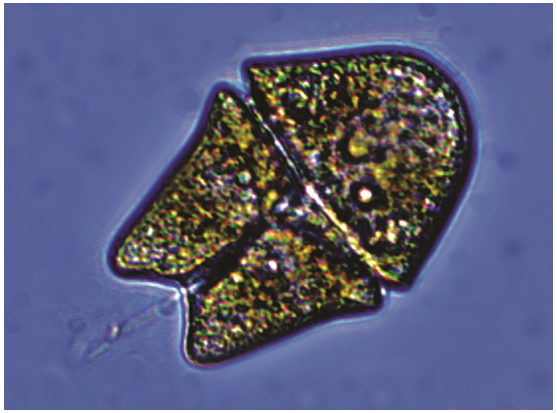


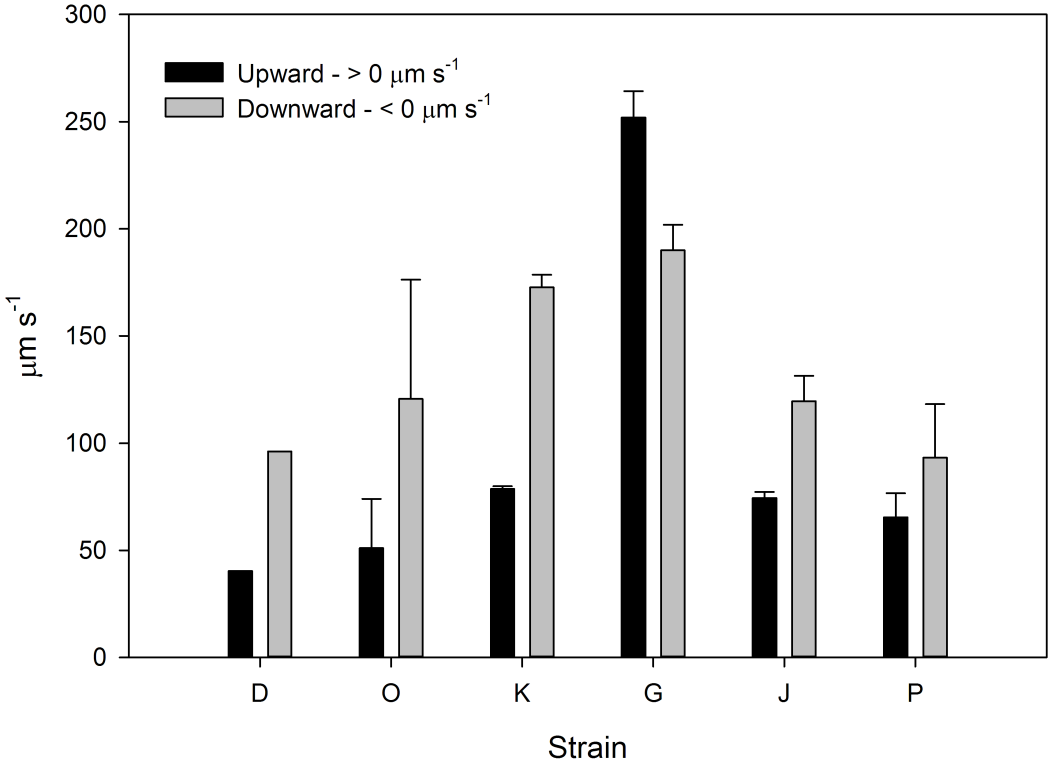
Paradox

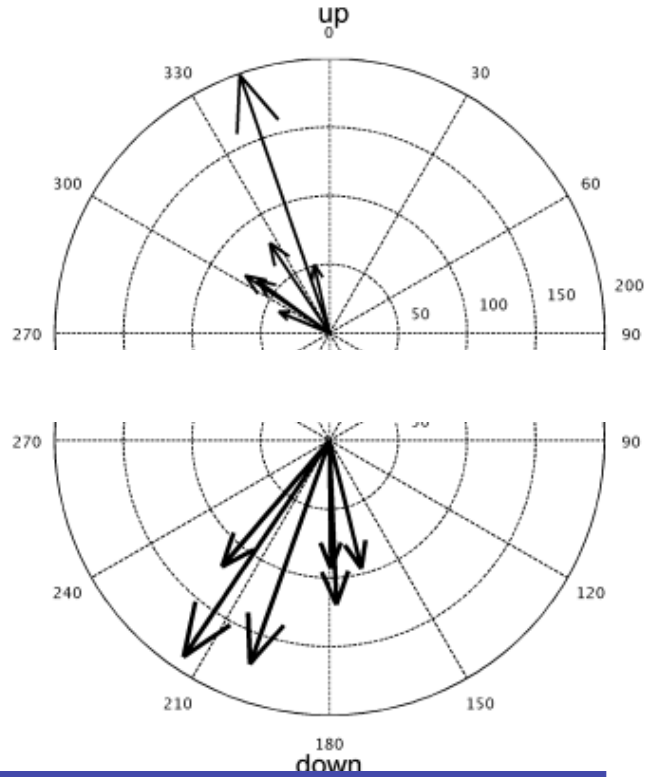
Harvey et al, 2015

Pervasive intra-specific variability…

- variable motility across strains of *Akashiwo sanguinea*





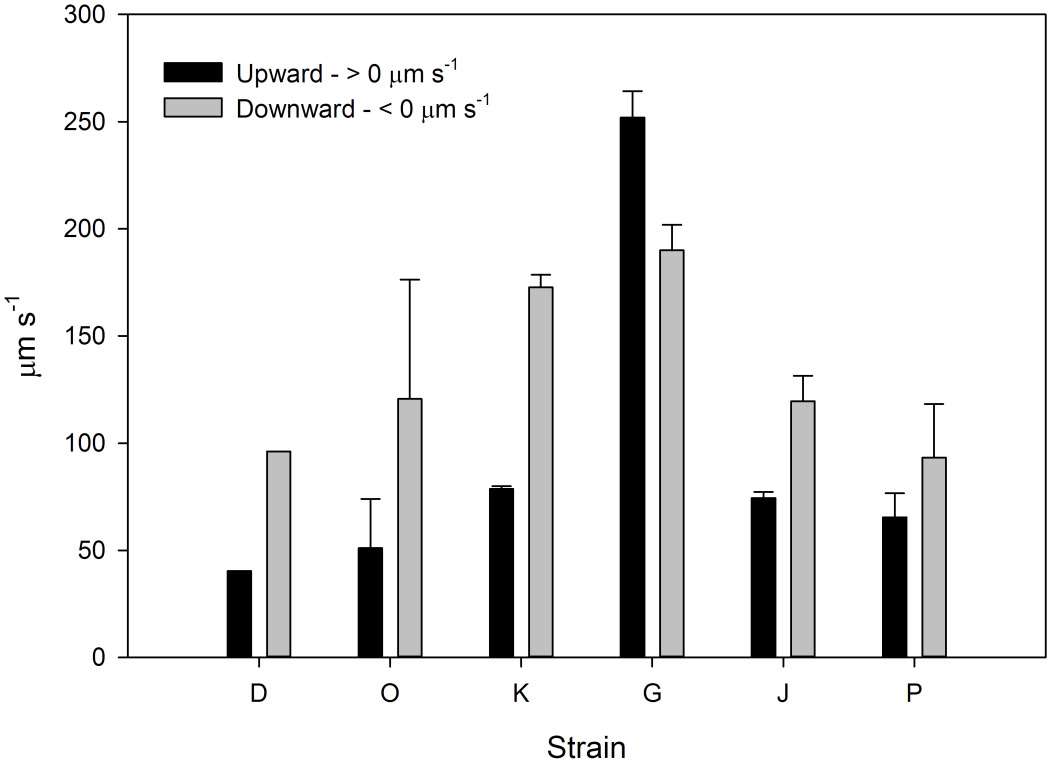


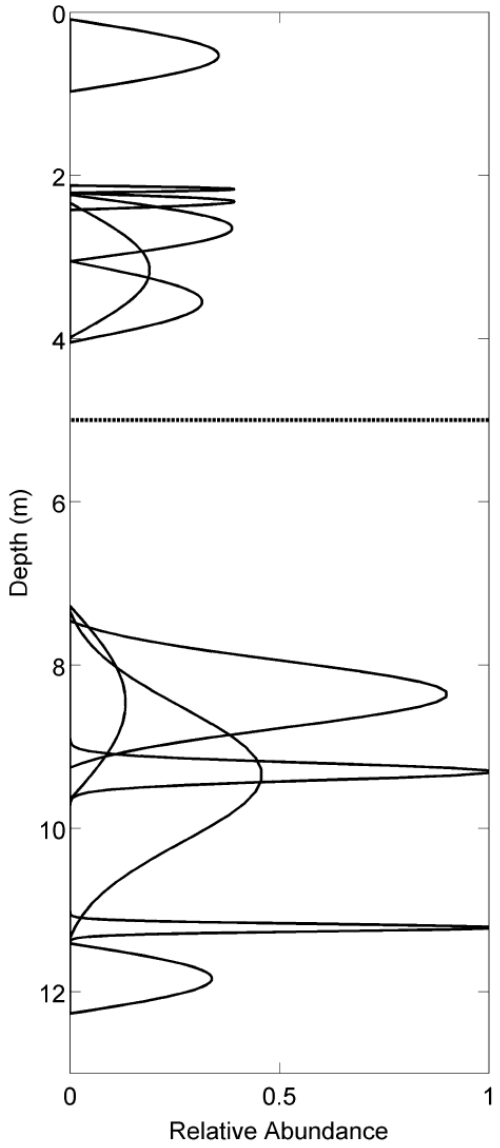
Paradox

Menden-Deuer & Montalbano 2015

Pervasive intra-specific variability…

- variable motility across strains of *Akashiwo sanguinea*



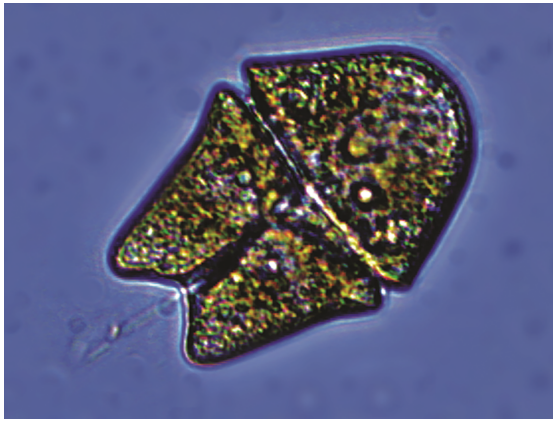


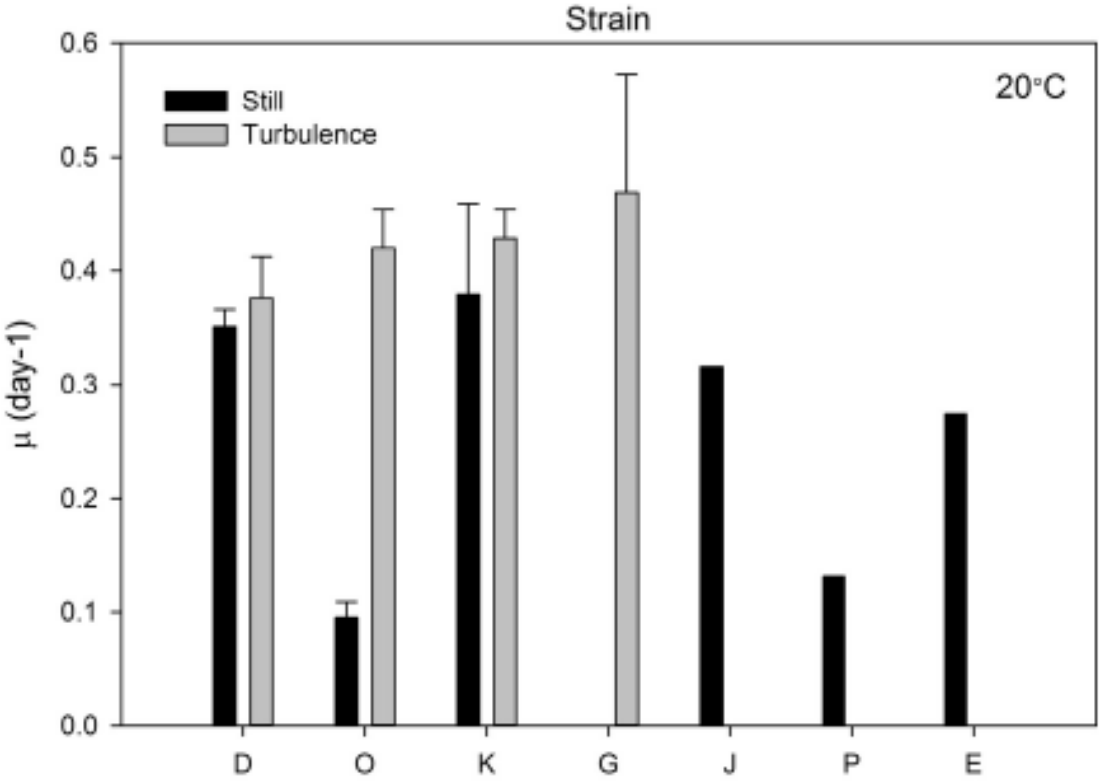
Paradox

Menden-Deuer & Montalbano 2015

Pervasive intra-specific variability…

- variable growth rates across strains of *Akashiwo sanguinea*

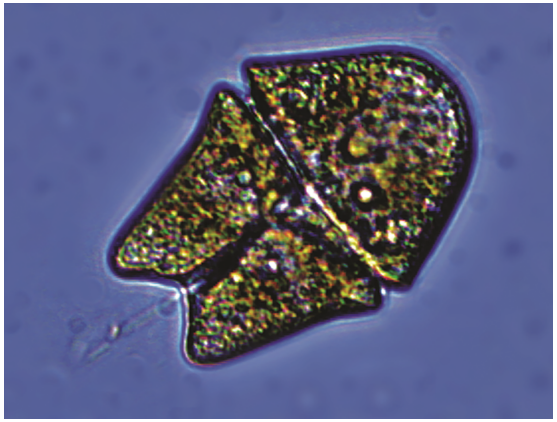


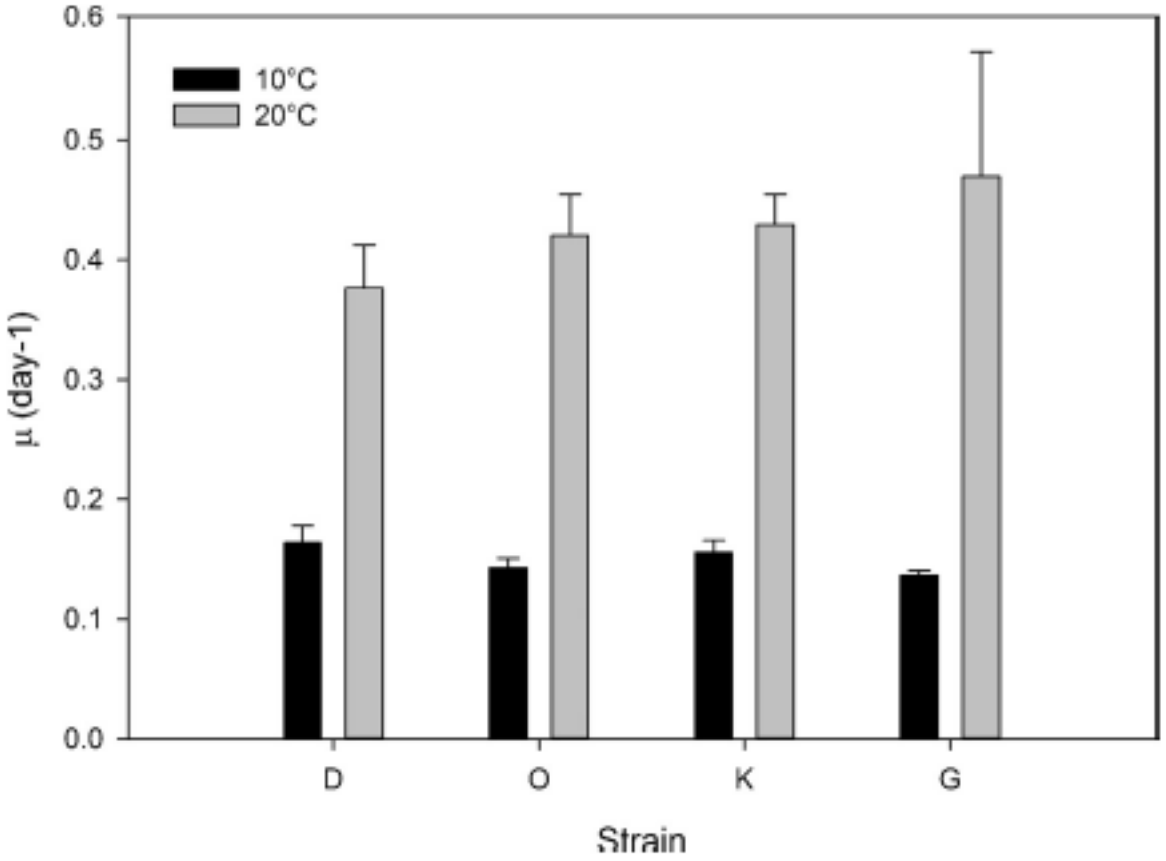


Paradox Menden-Deuer & Montalbano 2015

Pervasive intra-specific variability…

- but some organizing principles, e.g. temperature enhanced growth in strains of *Akashiwo sanguinea*





Paradox Menden-Deuer & Montalbano 2015

Pervasive intra-specific variability…

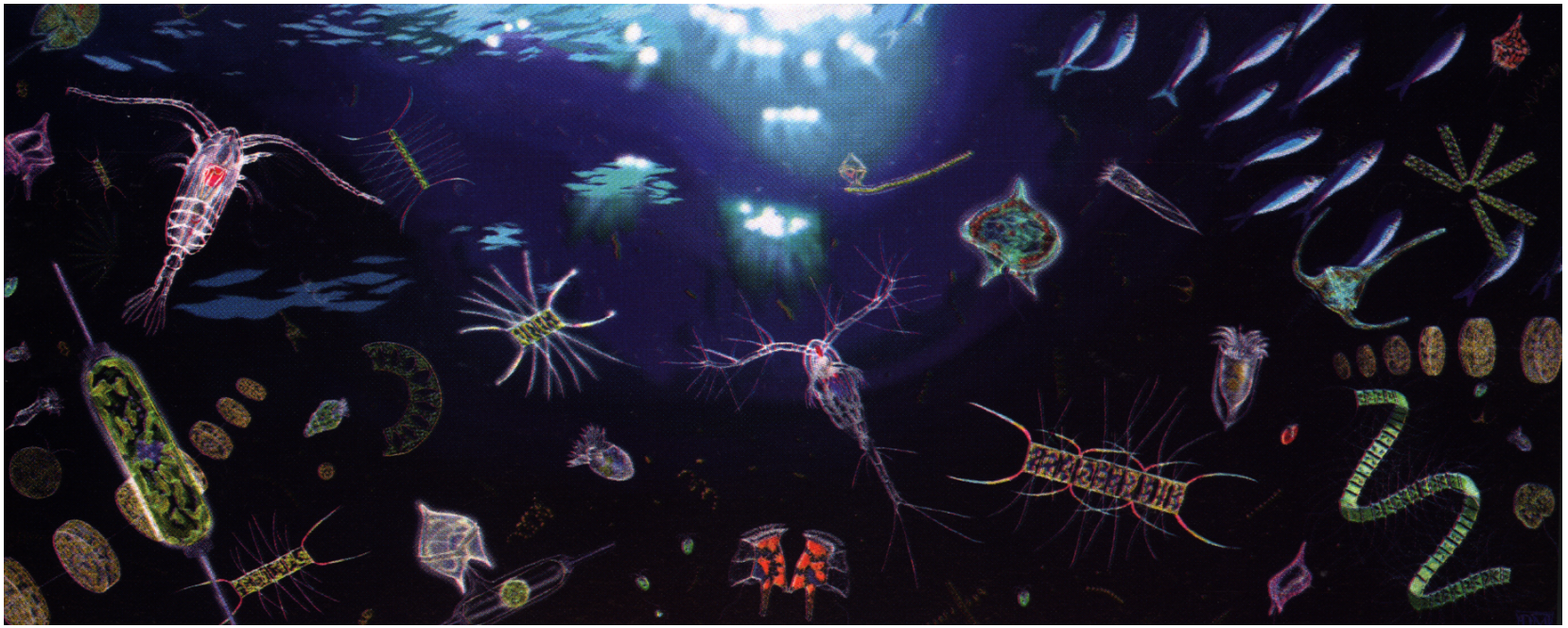
- chemical composition (Moal et al. 1987)
- thermal adaptation (Thomas et al. 2012)
- growth optima (Boyd et al. 2013)
- salinity tolerance (Brand 1984)
- nitrogen fixation (Hutchins et al. 2013)
- ocean acid response (Schaum et al. 2013)
- genetics (Rynearson & Armbrust 2004,Whittaker et al. 2012)

Empirical investigations of intra-specific variability in plankton physiology, genetics or behavior are rare but discoveries are frequent

Paradox of the Plankton

"How is it possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials?"

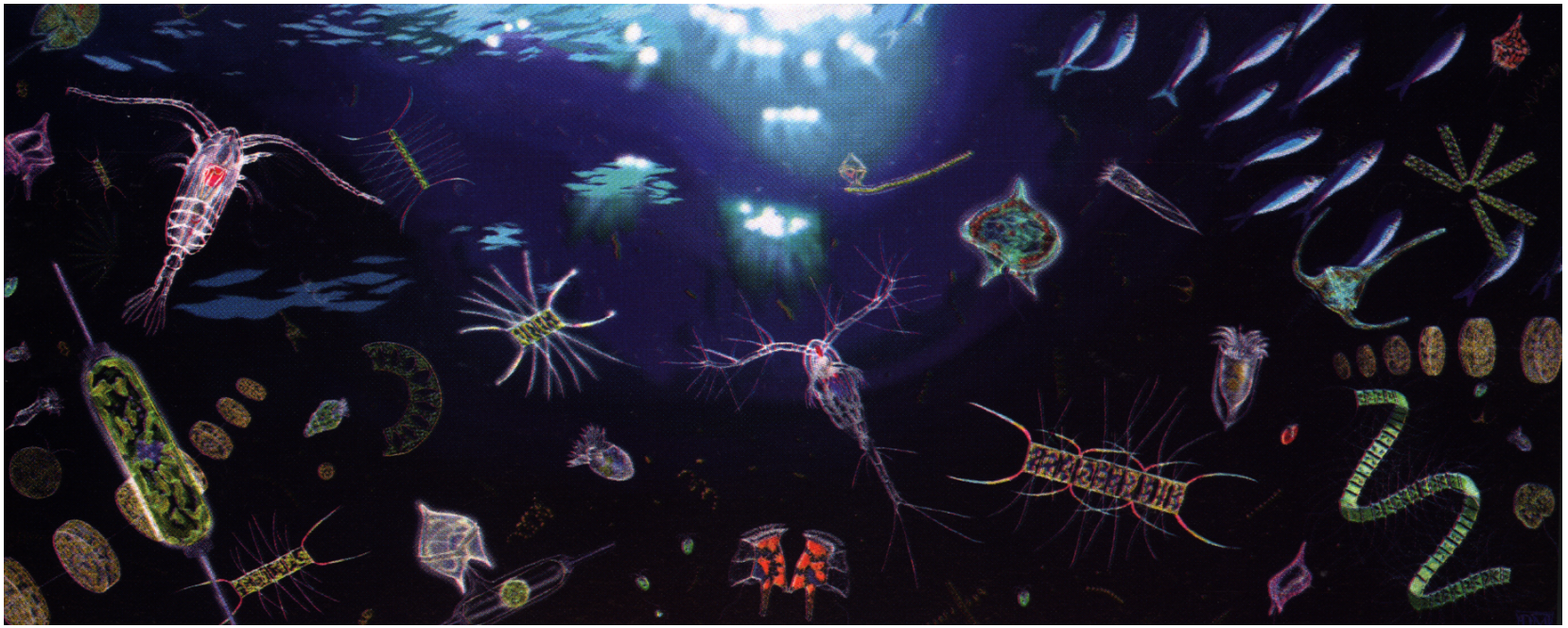
G. Evelyn Hutchinson 1961



Paradox of the Plankton

"How is it possible for a number of species - with high intra-specific variability - to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials?"

G. Evelyn Hutchinson 1961



Many hypotheses advanced

- resource ratio hypothesis (Tilman 1977, 1994)

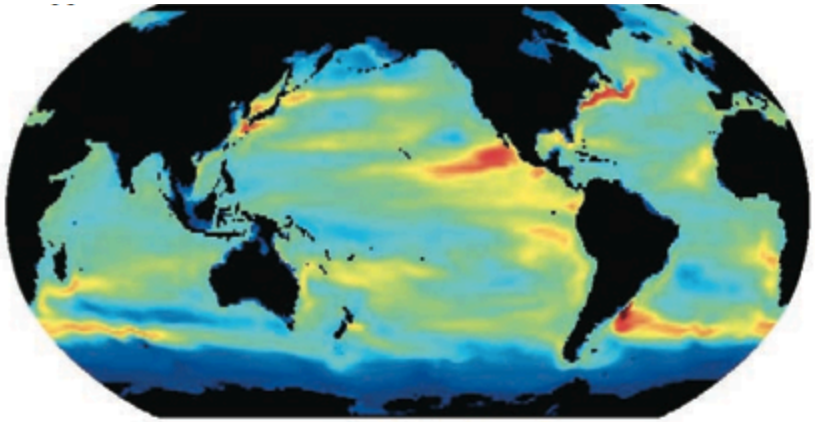
- chaotic oscillations (Huisman Weissing 1999)

- chaotic fluid motion (Pentek et al. 2000)

- localized competition (Kerr et al. 2002)

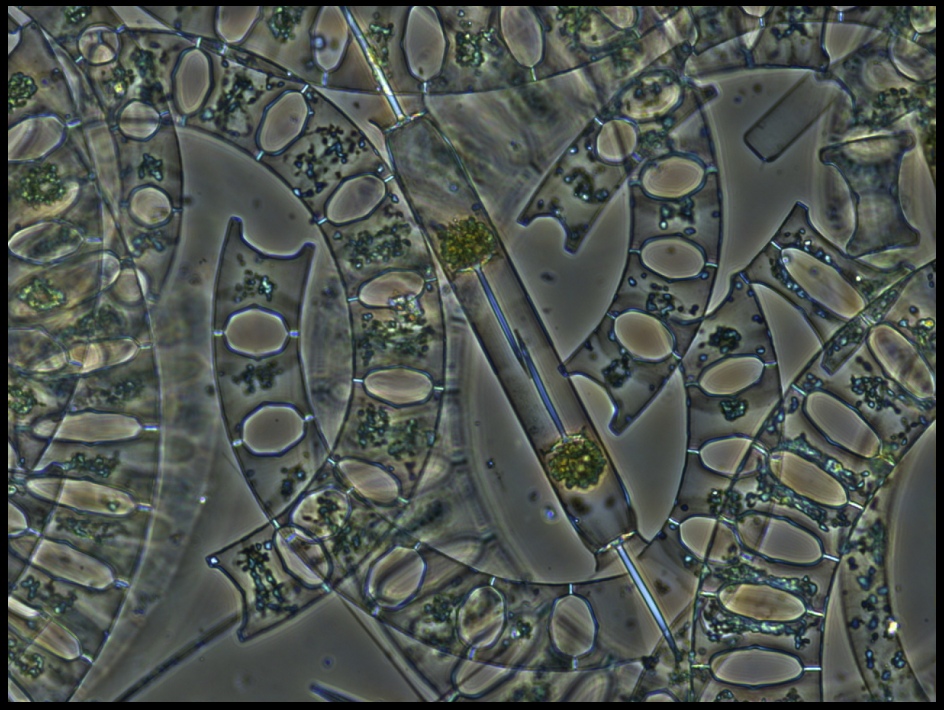
- predation/competition (Record et al. 2013, Cropp and Norbury 2012)

- latitudinal/seasonal gradients (Barton et al. 2010)



Species interactions are cell-cell interactions

outcomes of ecological interactions are measured at the population level: abundance, growth rate, distribution
- the processes that result in population dynamics occur at the individual level: feeding, motility, resource uptake, sex



Game theory

- examines outcomes of competitions based on individual interactions
- outcomes depend on behavior of individual players

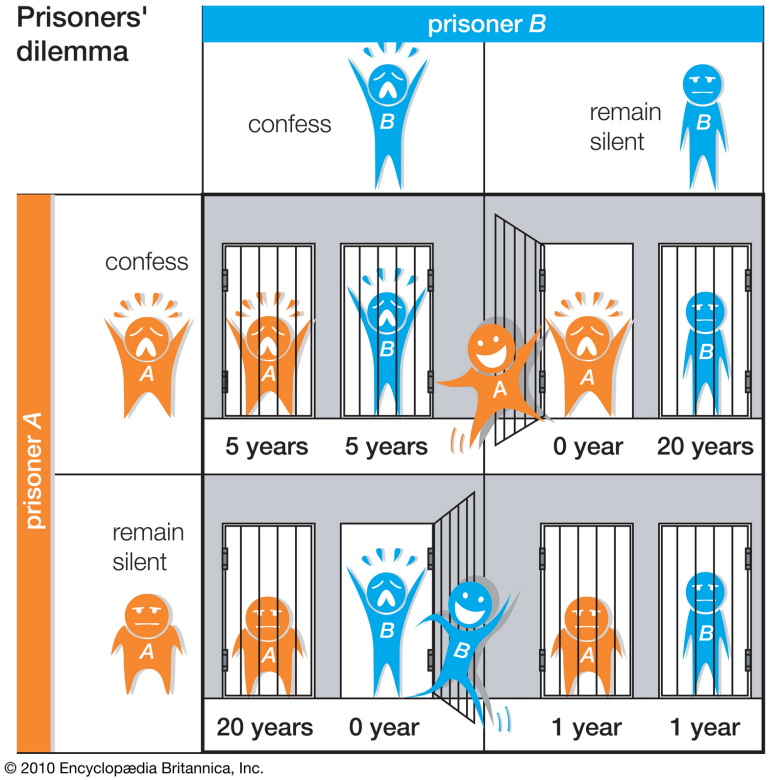
P2 \ P1	W	L
W	(0, 0)	(1, –1)
L	(–1, 1)	(0, 0)

Game theory

- examines outcomes of competitions based on individual interactions
- outcomes depend on behavior of individual players

- Prisoner's dilemma famous example:

P2 \ P1	W	L
W	(0, 0)	(1, –1)
L	(–1, 1)	(0, 0)



Competition with intra-specific variability

Model simulation set up

- individual based competition model of 2+ species

- intra-specific variability expressed as probability distribution of traits

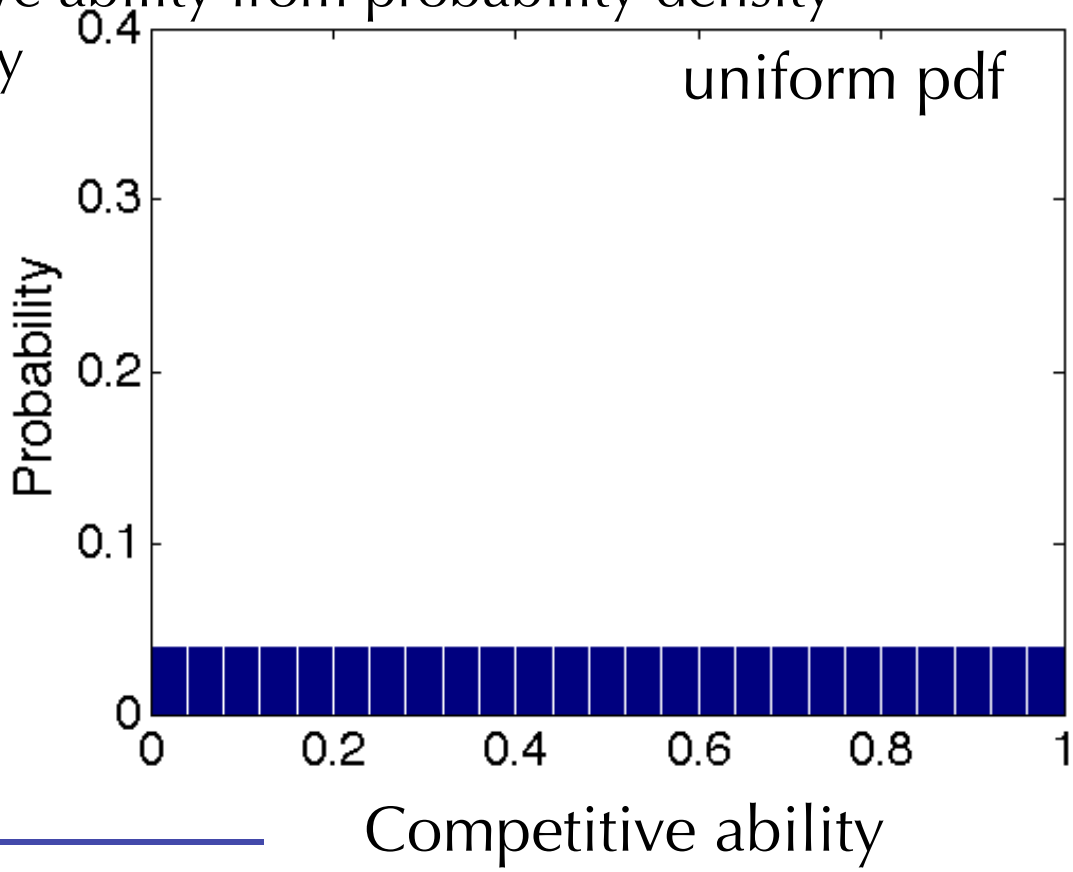
- randomly choose: competitive ability from probability density function that reflects variability

- all species have identical mean

- up to 10,000 individuals per species

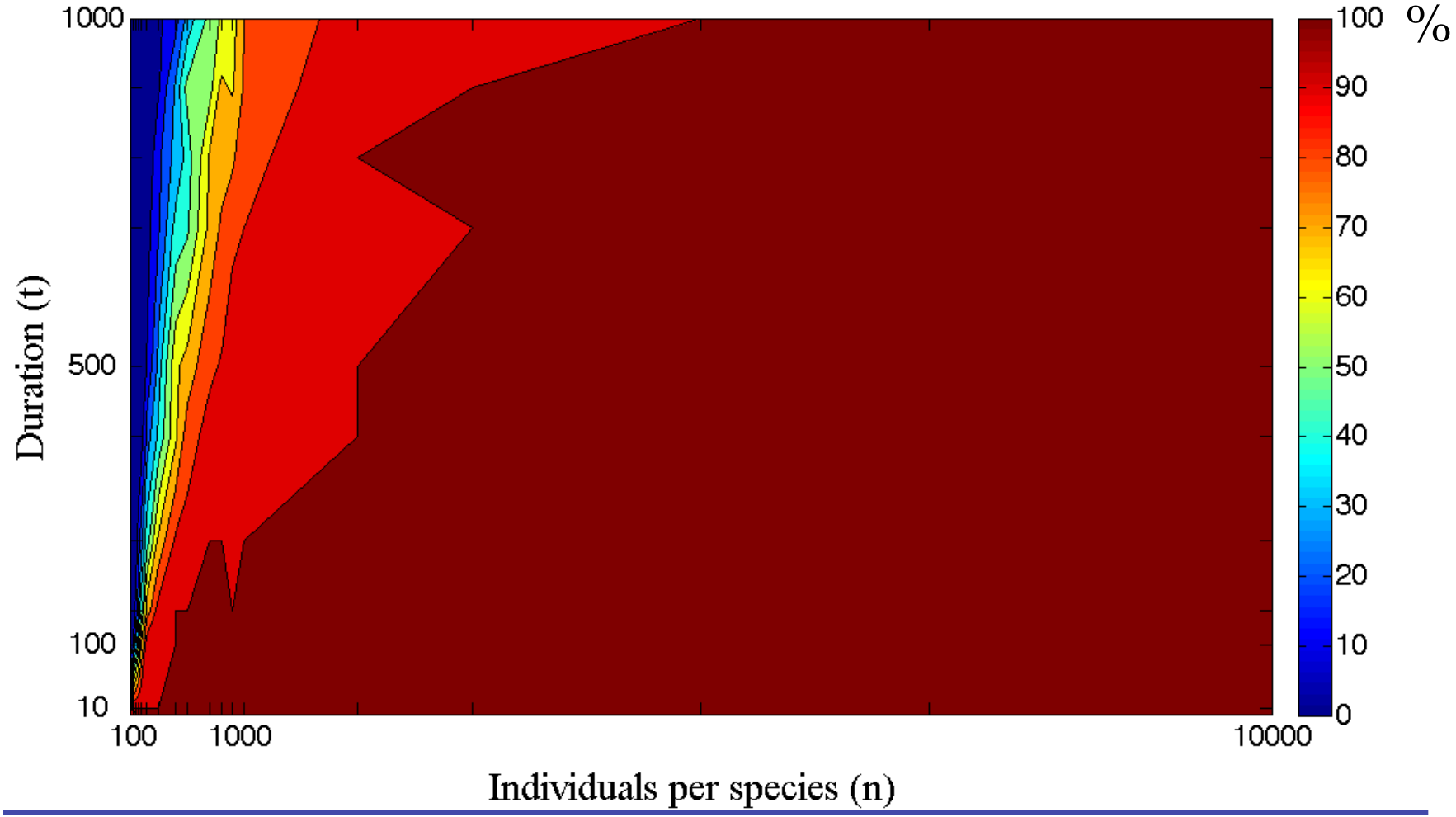
- up to 10,000 generations

- variable species have stronger and weaker competitors



Persistence in 2+-species competition

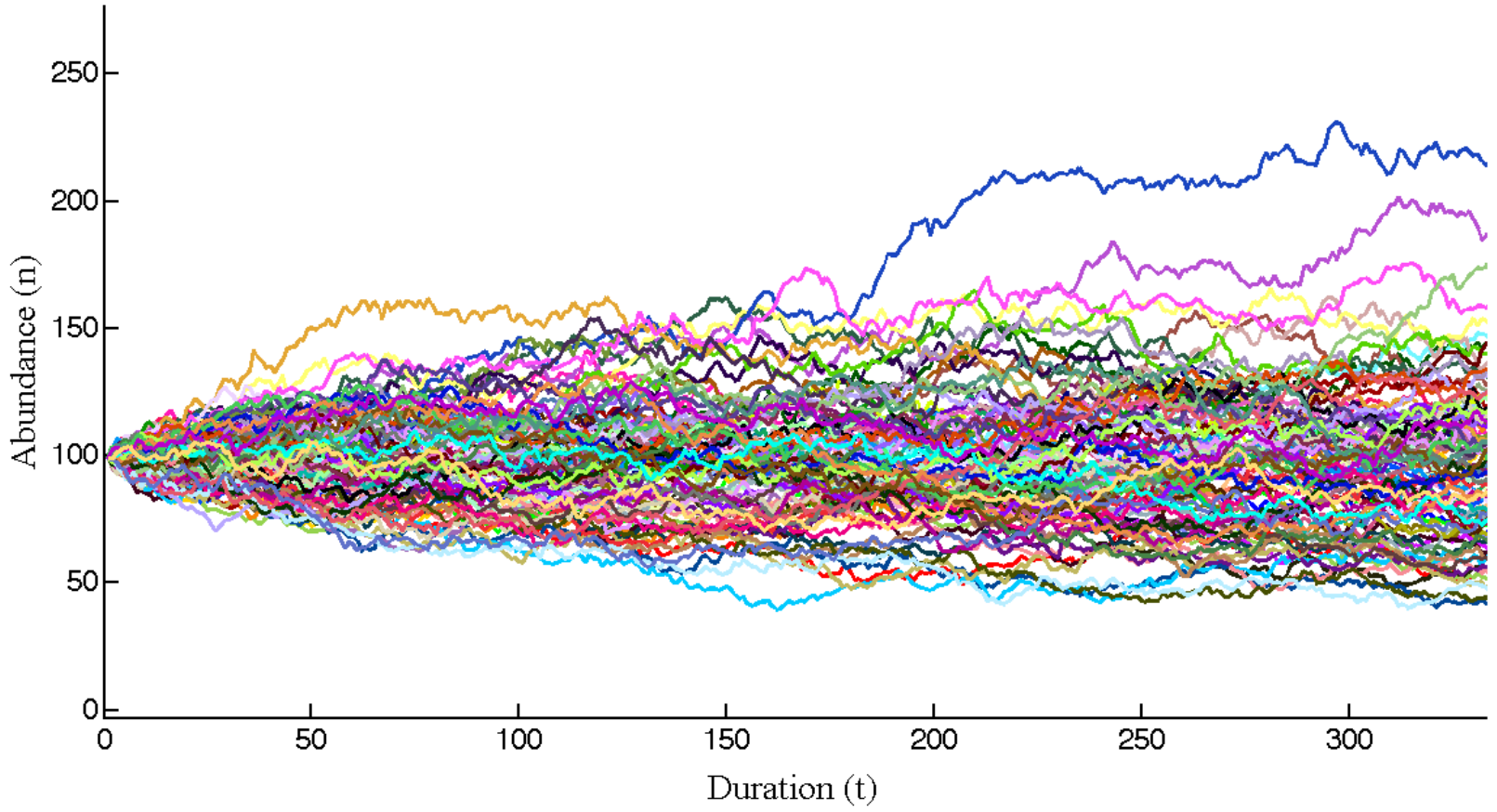
- frequency of 2 species persisted in 100 repeated, randomized simulations as a function of population size and duration



Paradox *Menden-Deuer & Rowlett 2014*

Persistence in multi-species competition

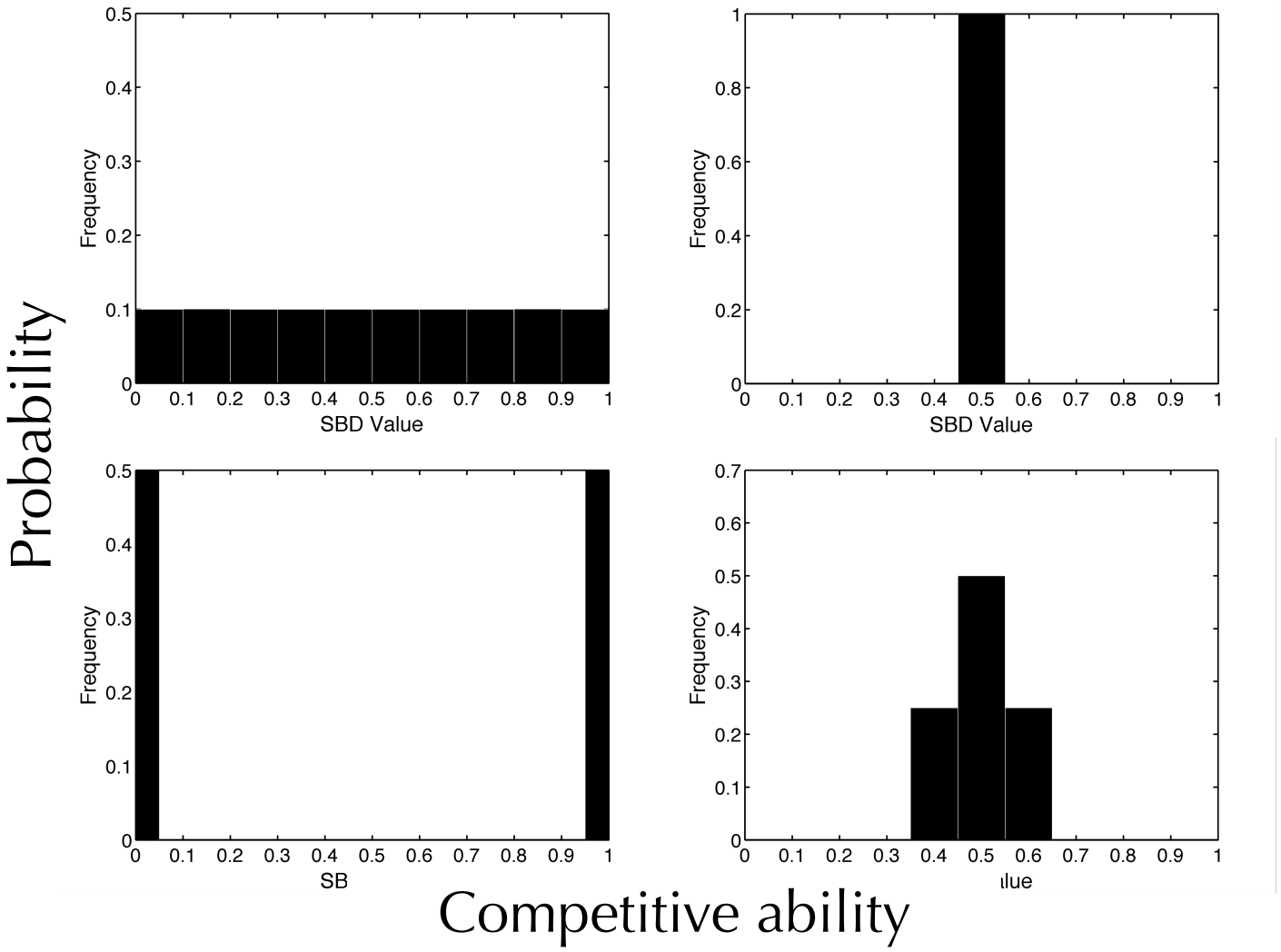
- population abundance over time in repeated, multi species competitions
- more than 100 coexisting species/strains/types



Paradox *Menden-Deuer & Rowlett in prep.*

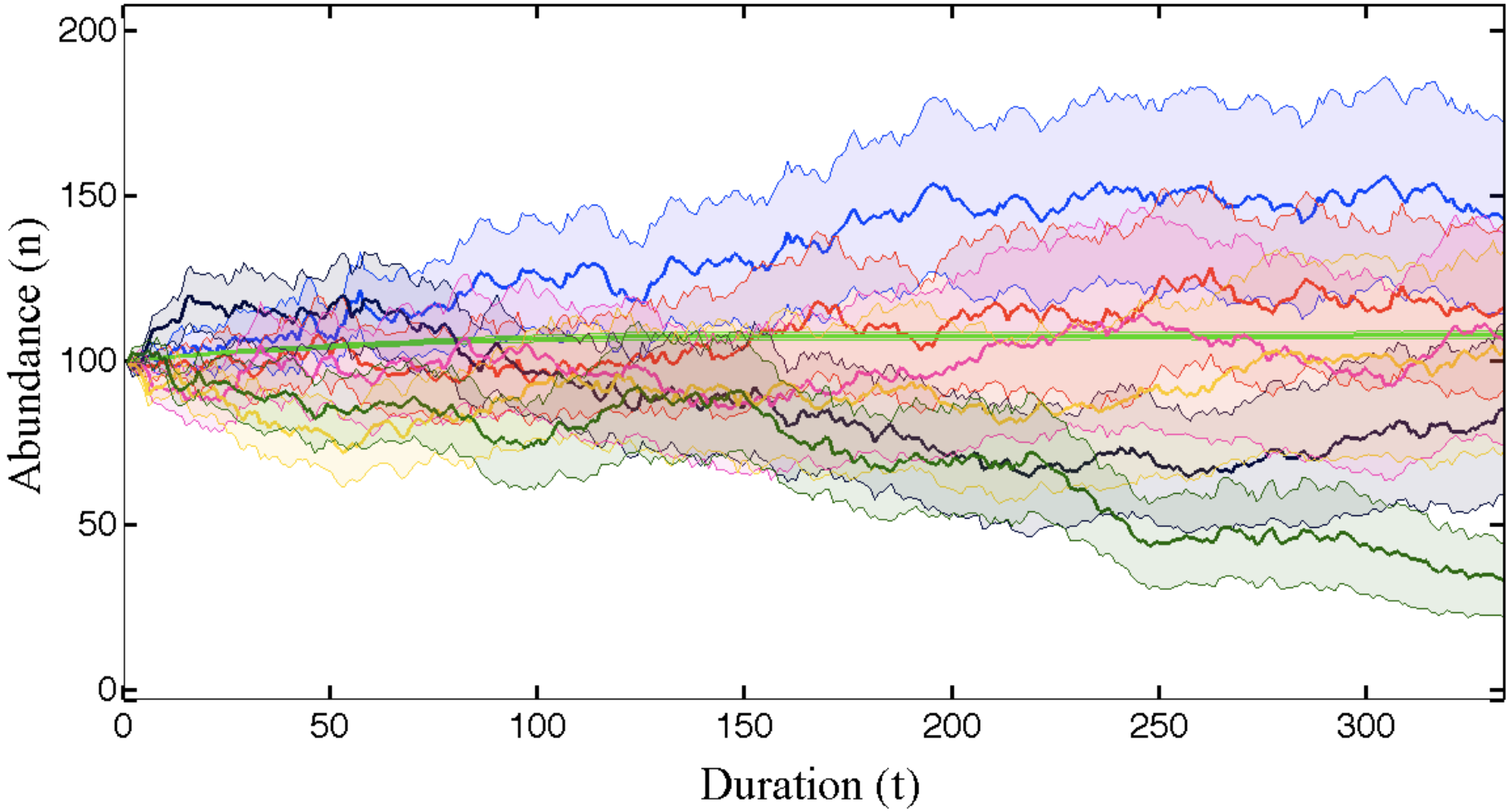
Competition with intra-specific variability

Does the degree and type of intra-specific variability matter?
What about species invasion or new species arising?



No disadvantage to variability

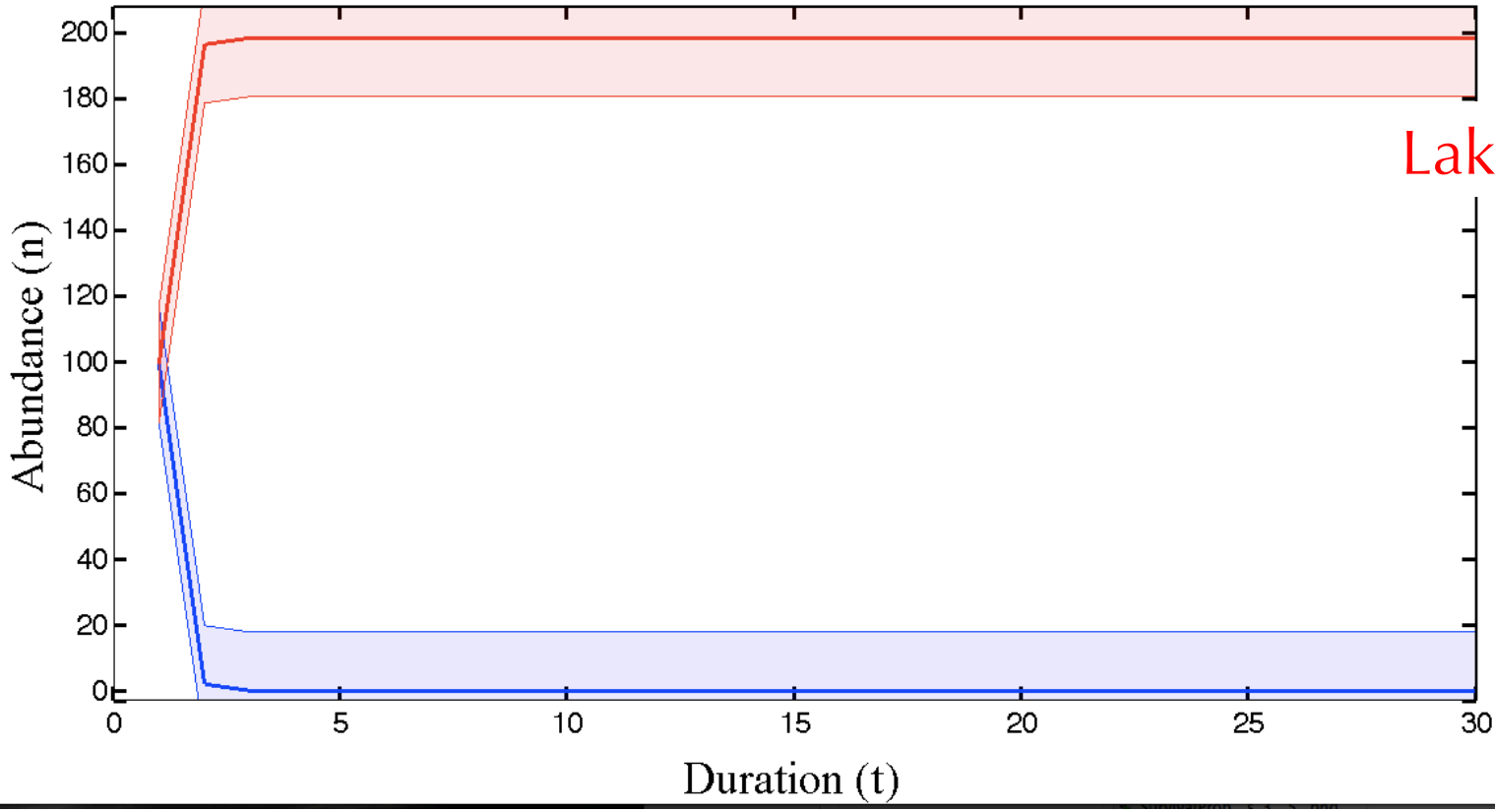
- Species with diverse behavior distributions survive in multi-species competition experiments – all have equal mean competitive ability



Paradox *Menden-Deuer & Rowlett in prep.*

Lack of variability can be an Achilles heel

- Invariant competitor (blue) goes extinct quickly against variable competitor (red)
- both have equal mean competitive ability



Lake Wobegon

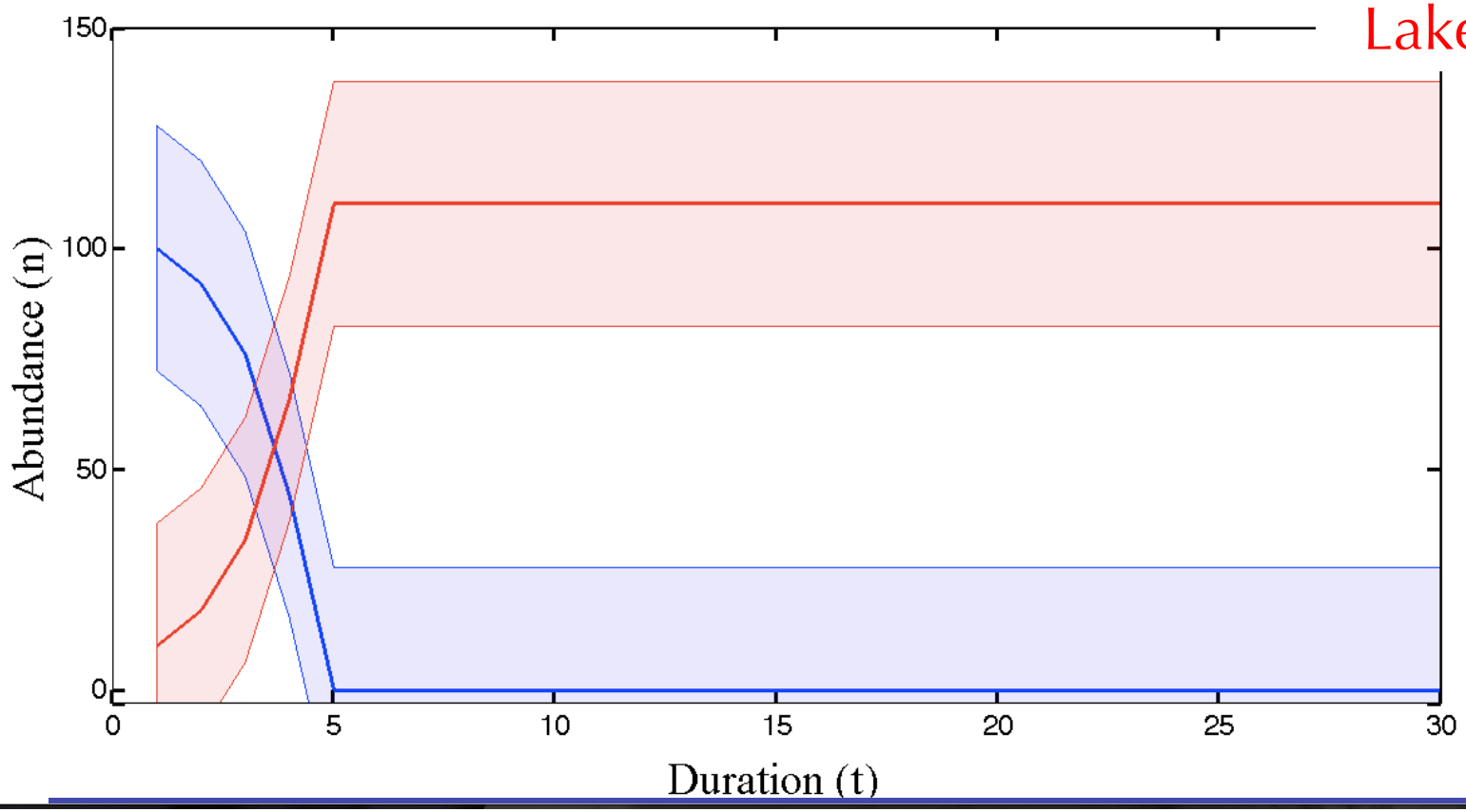
Invariant

Paradox

Menden-Deuer & Rowlett in prep.

Lack of variability can be an Achilles heel

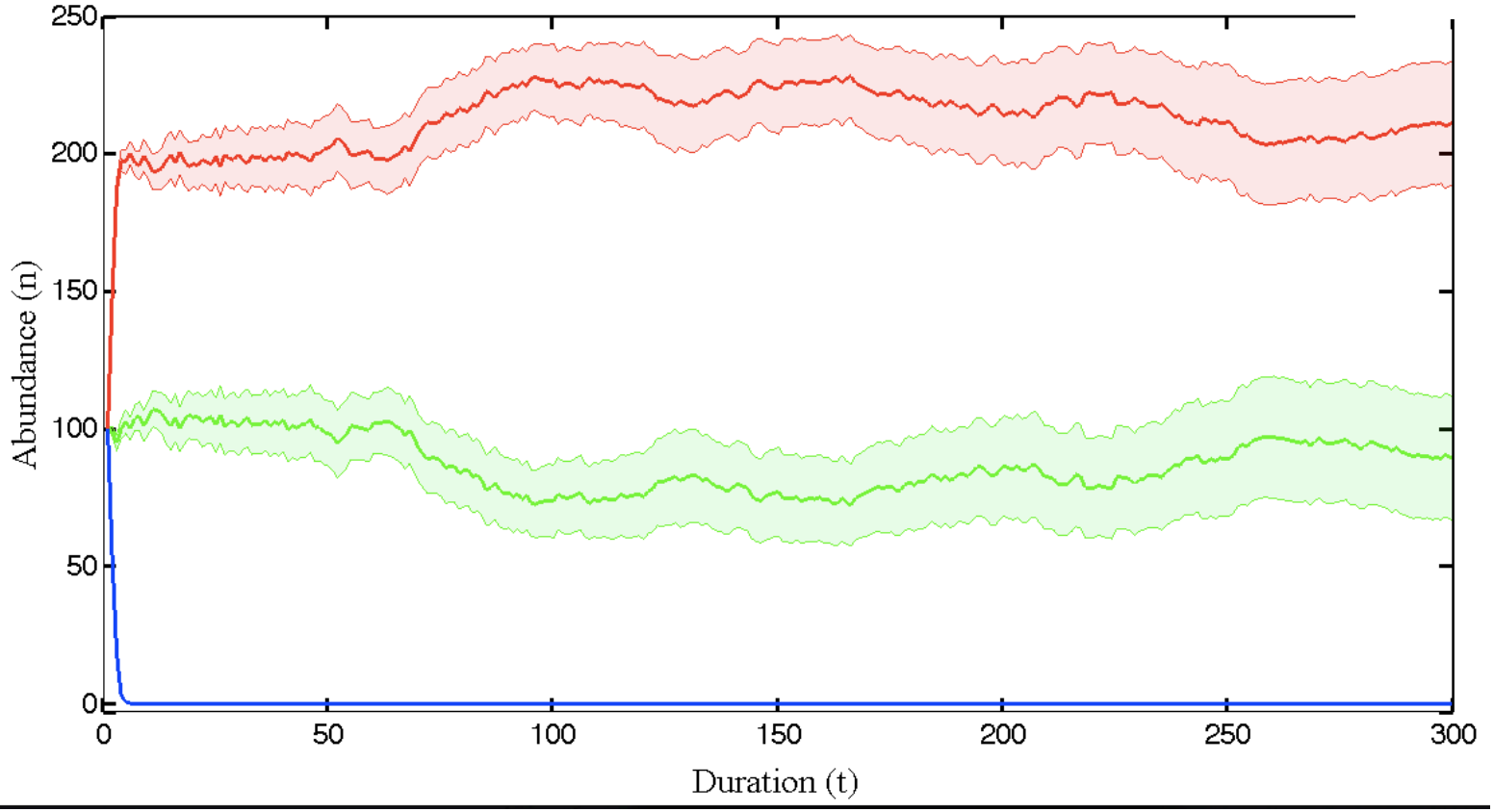
- Invariant competitor (blue) can even be displaced by invading variable competitor (red)
- both have equal mean competitive ability



Paradox

Menden-Deuer & Rowlett in prep.

Variability triumphs in competition

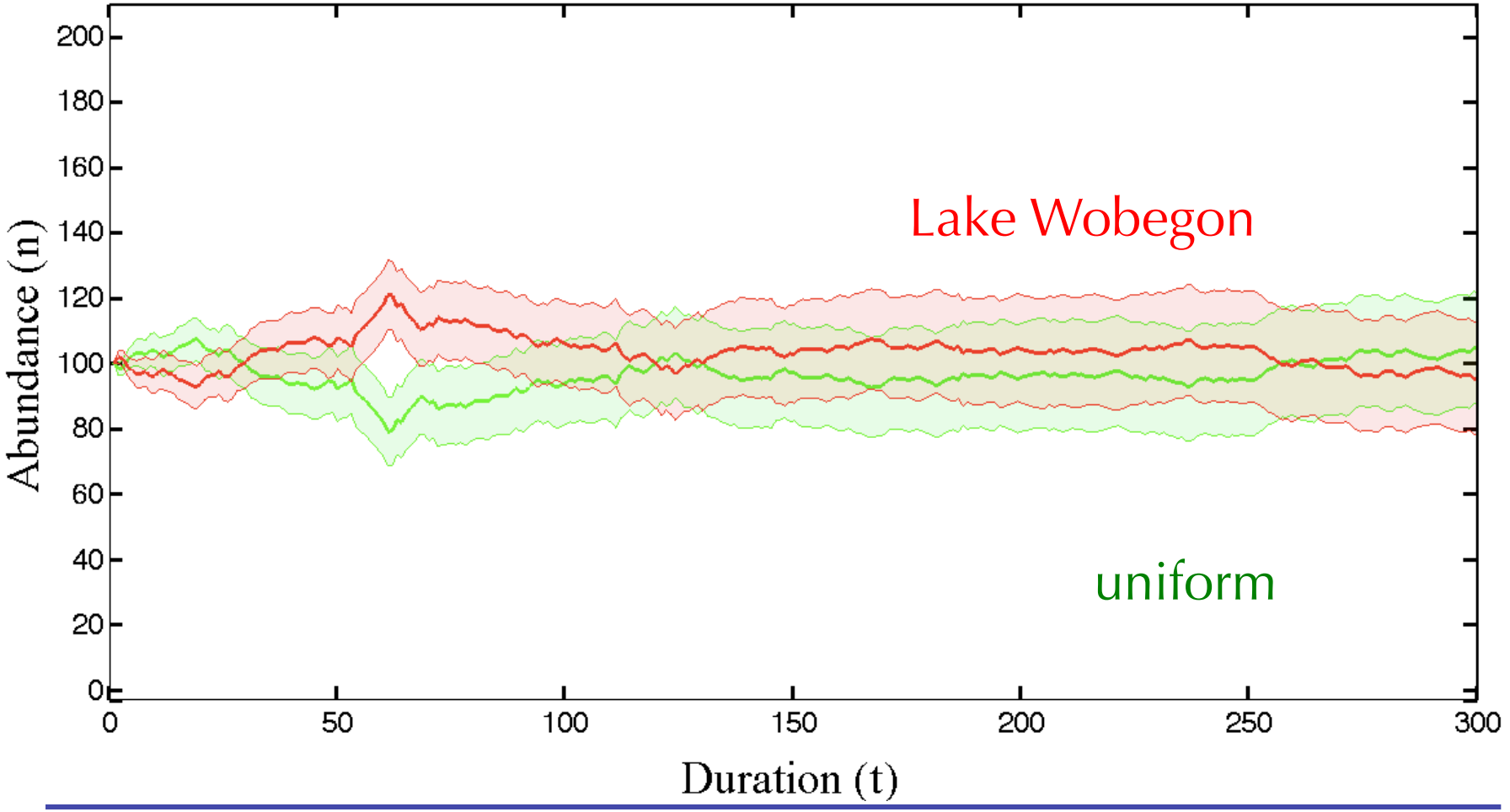


Paradox

Menden-Deuer & Rowlett in prep.

Variability triumphs in competition

- uniform competitor persist against competitor that eliminated invariant competitor

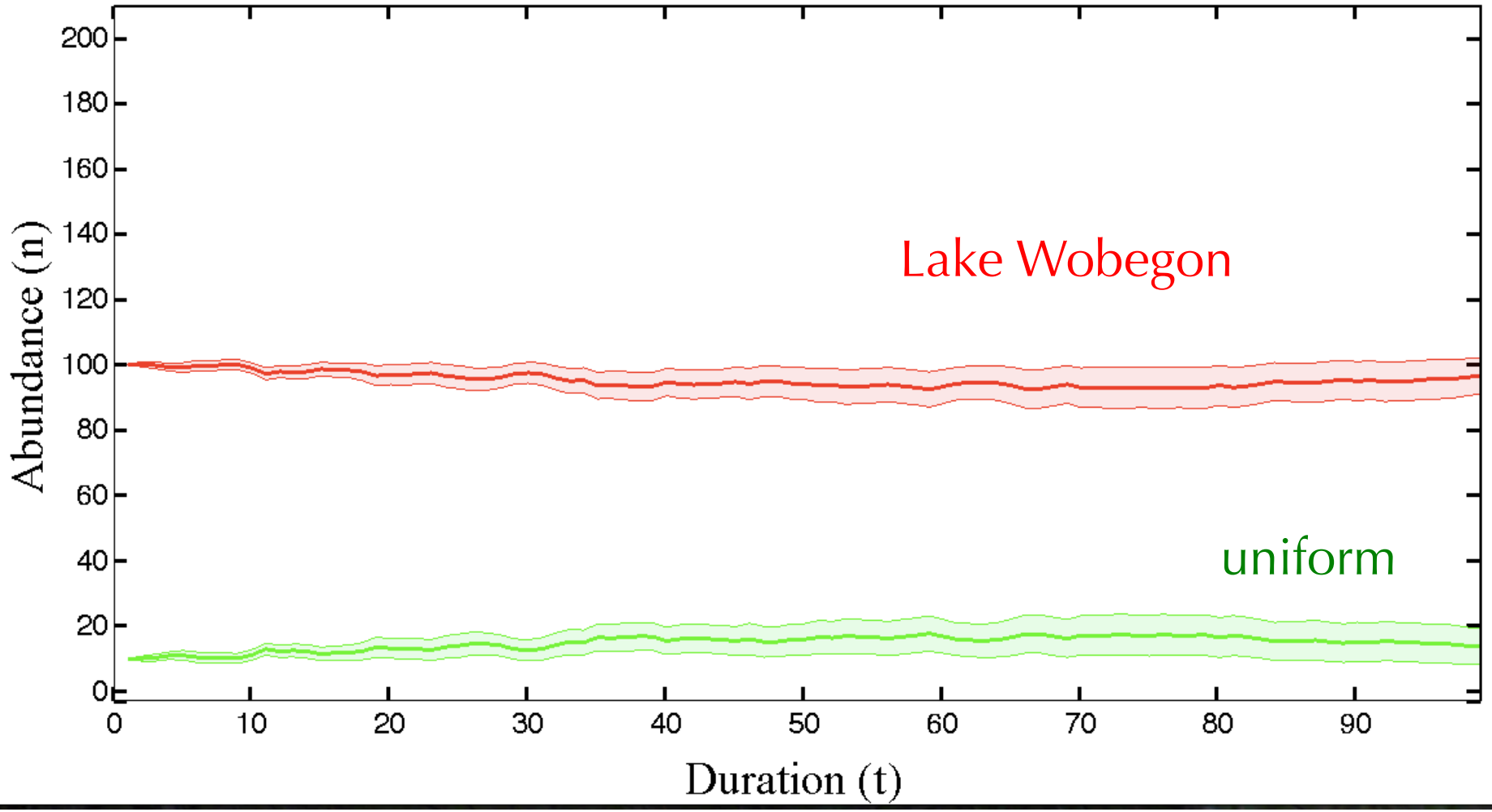


Paradox

Menden-Deuer & Rowlett in prep.

Variability triumphs in competition

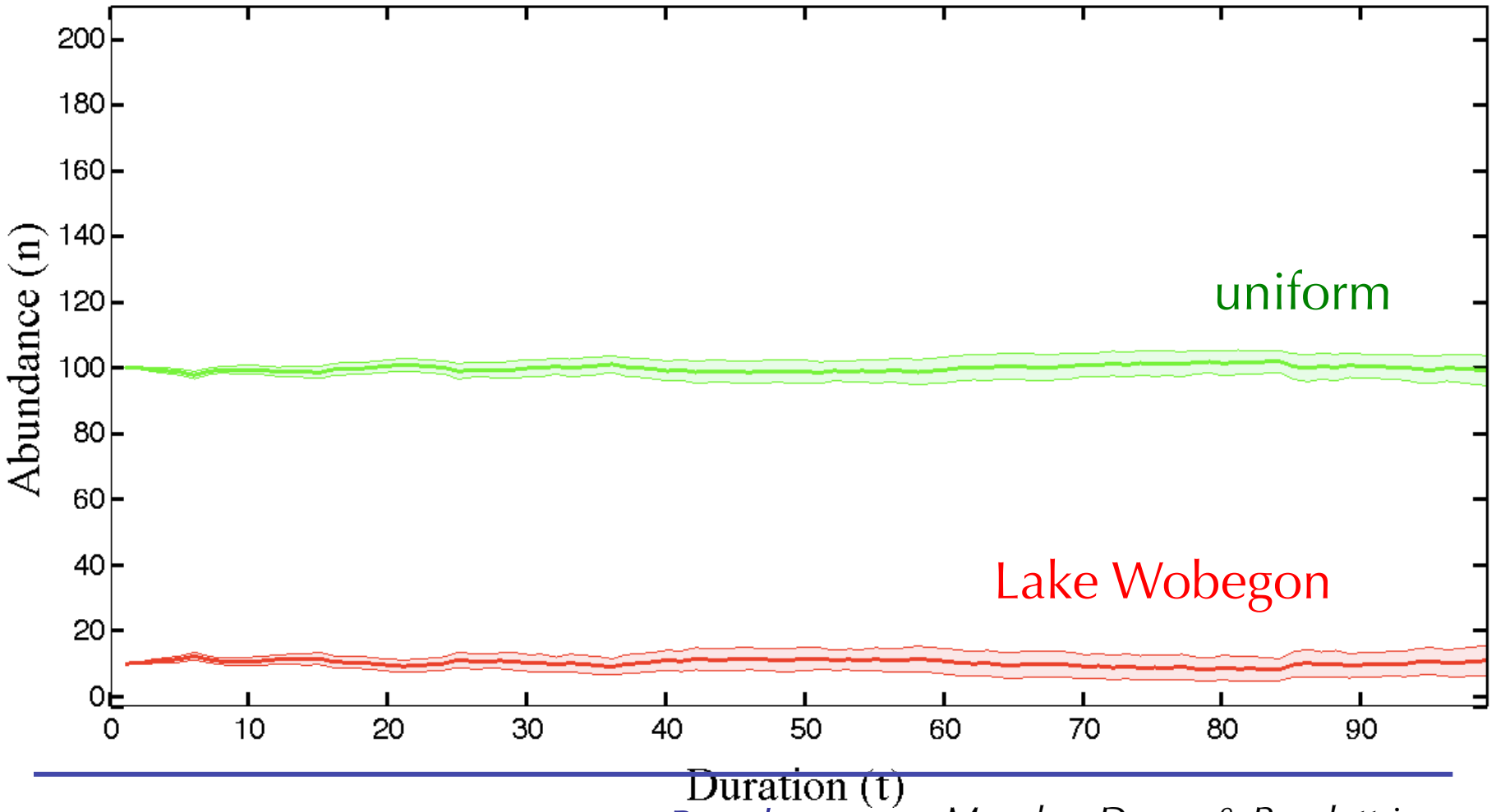
- *uniform competitor can maintain inferior population abundance*



Paradox *Menden-Deuer & Rowlett in prep.*

Variability triumphs in competition

- *uniform competitor can not be invaded*



Paradox

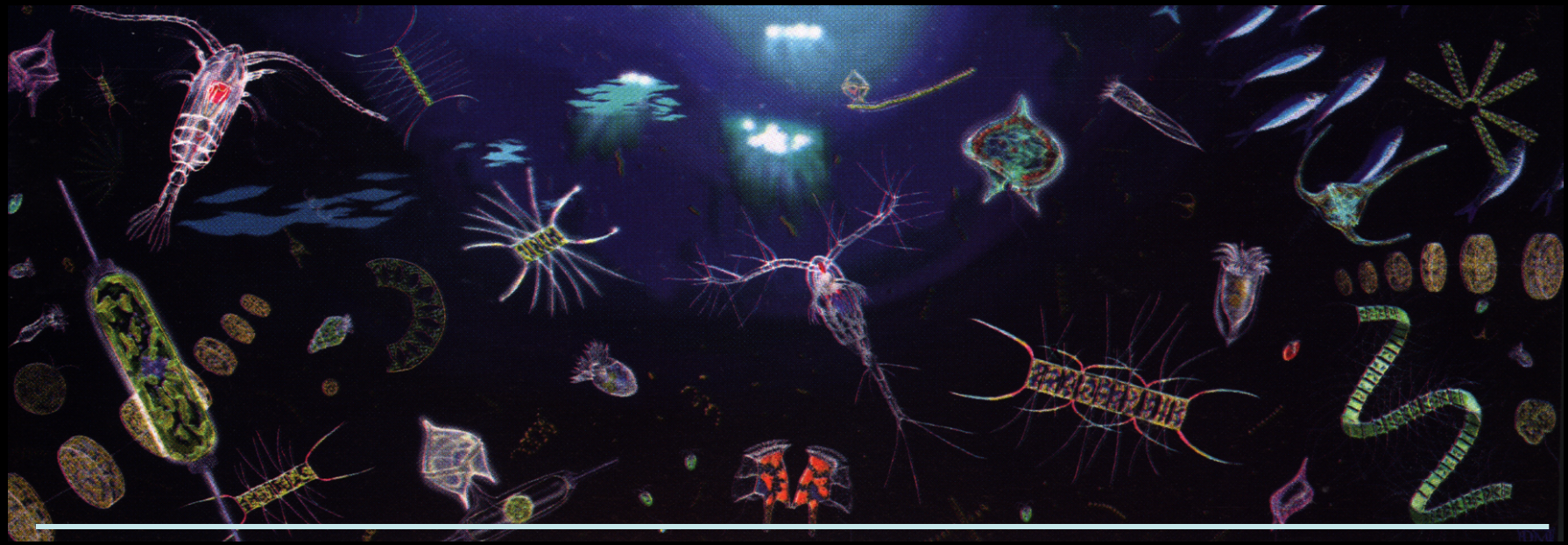
Menden-Deuer & Rowlett in prep.

Testable Hypotheses

- strains/species should have variable physiology, behavior

- established species that resist invasion likely hypervariable

- examine trade off between benefit of intra-specific variability and selective advantage of drive towards less variable but higher competitive ability



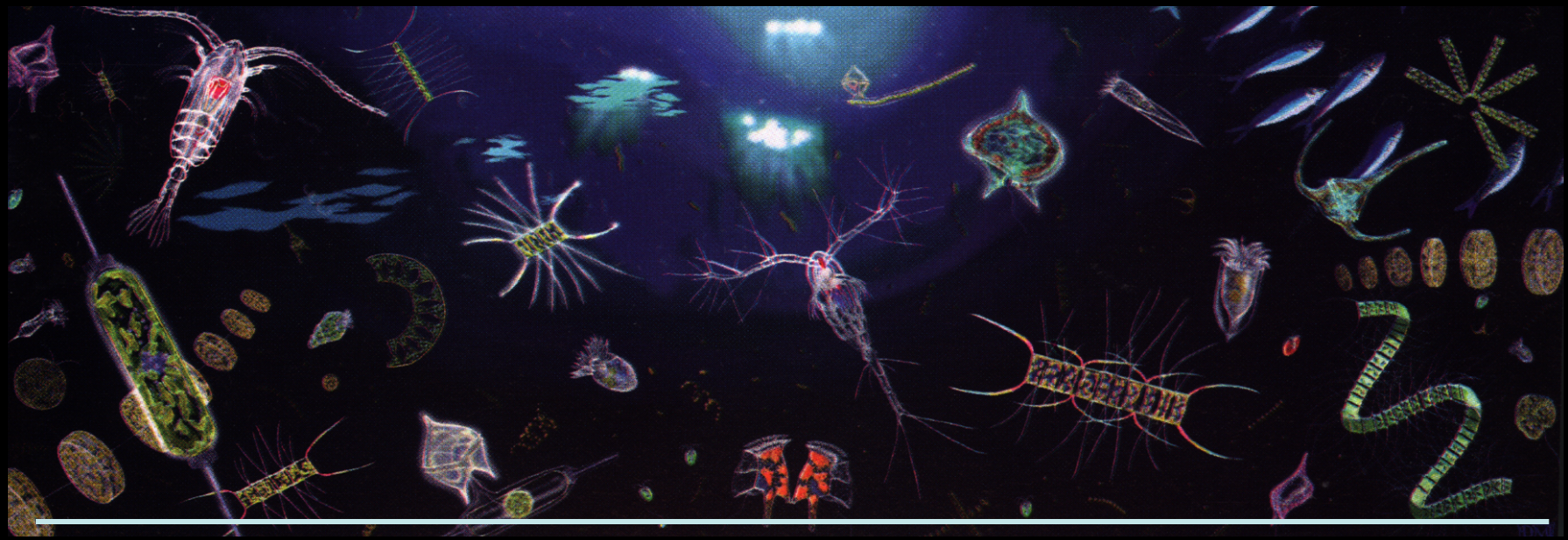
Paradox D. Jacobsen, 1999

Conclusions/Implications

- incorporation of intra-specific variability supports coexistence, dynamic population abundances

- hyper-variable distribution resists invasion
- variability has adaptive value, independent of specific formulations: heterogeneity, no. of nutrients

- intra-specific variability may be a mechanism for marine microbes to acclimate and ultimately adapt to changing ocean



Paradox D. Jacobsen, 1999

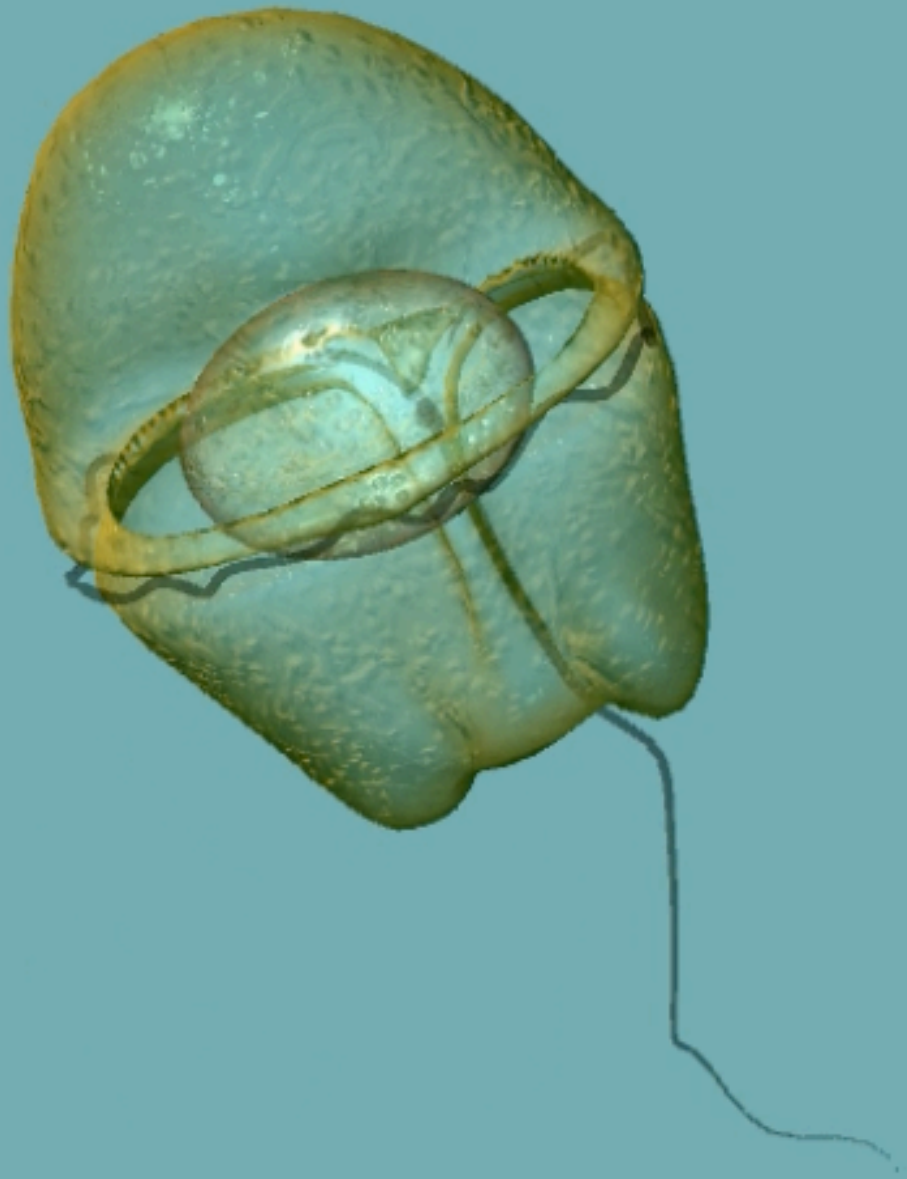
Thank you

Post-doc Position available

Plankton predator prey interactions

Dennis Hlynsky

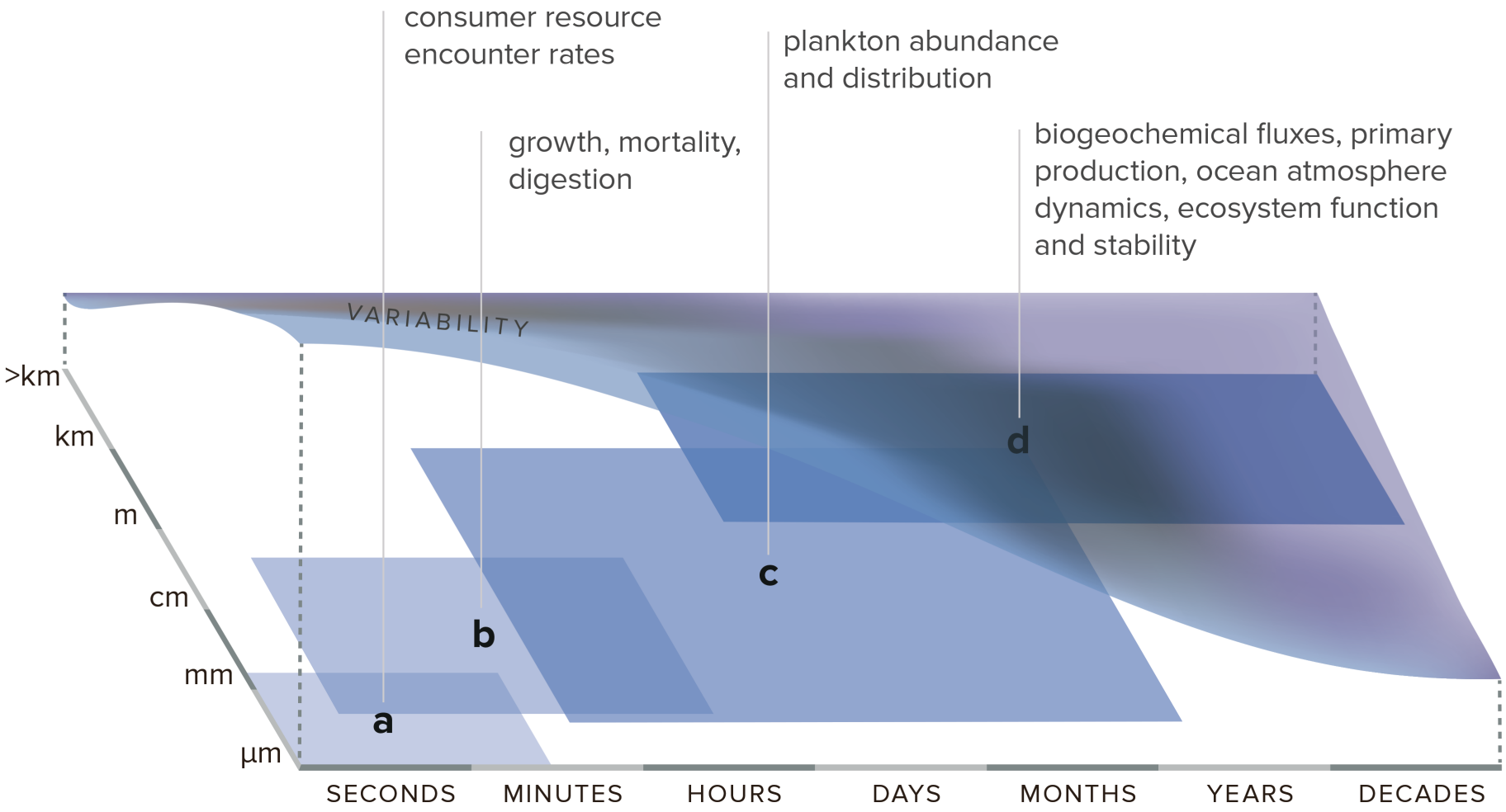
Rhode Island School of Design



Dennis Hlynsky

Rhode Island School of Design

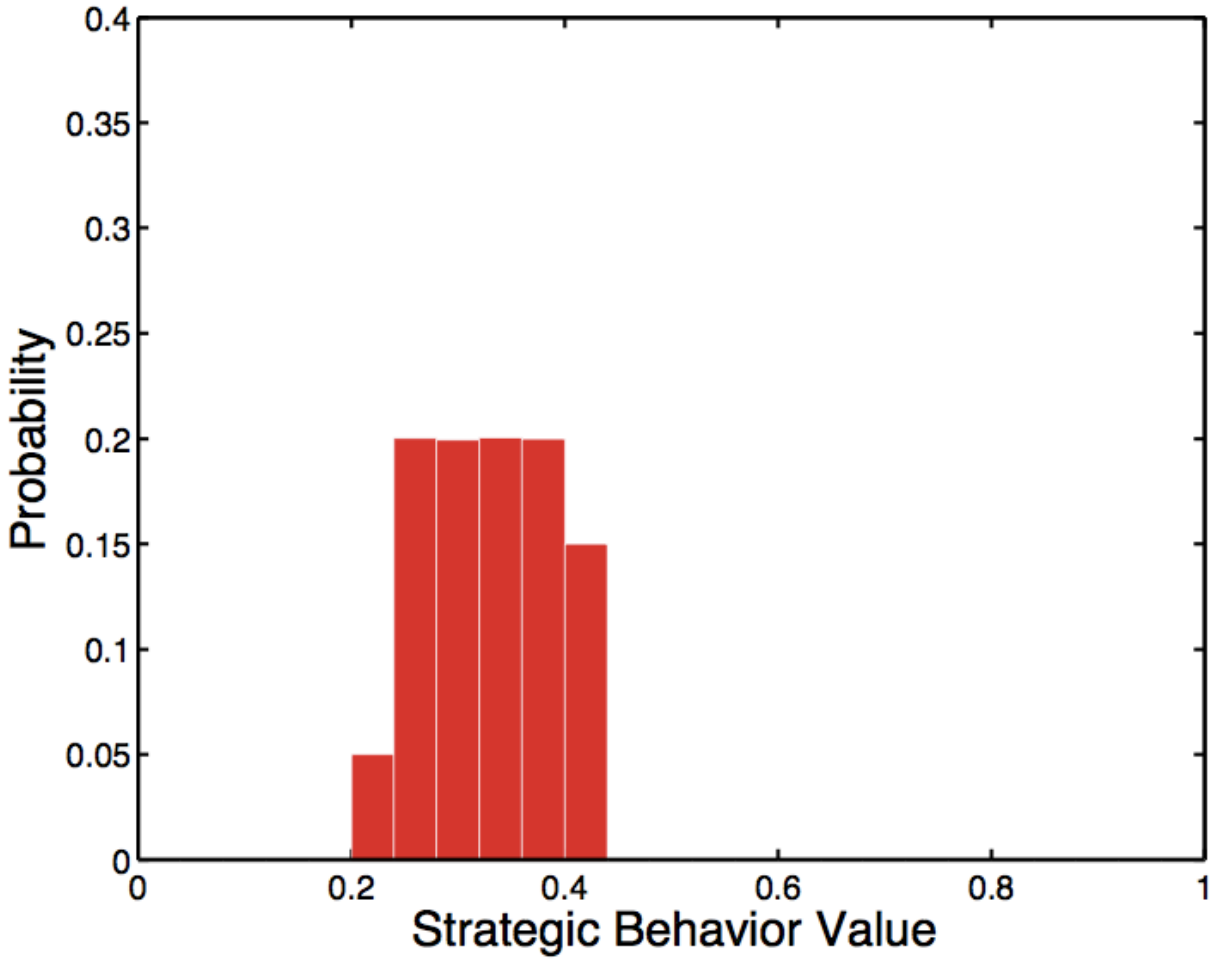
Variability an integral trait?



Paradox

Illustration Josh Wood
Rynearson & Menden-Deuer, in press

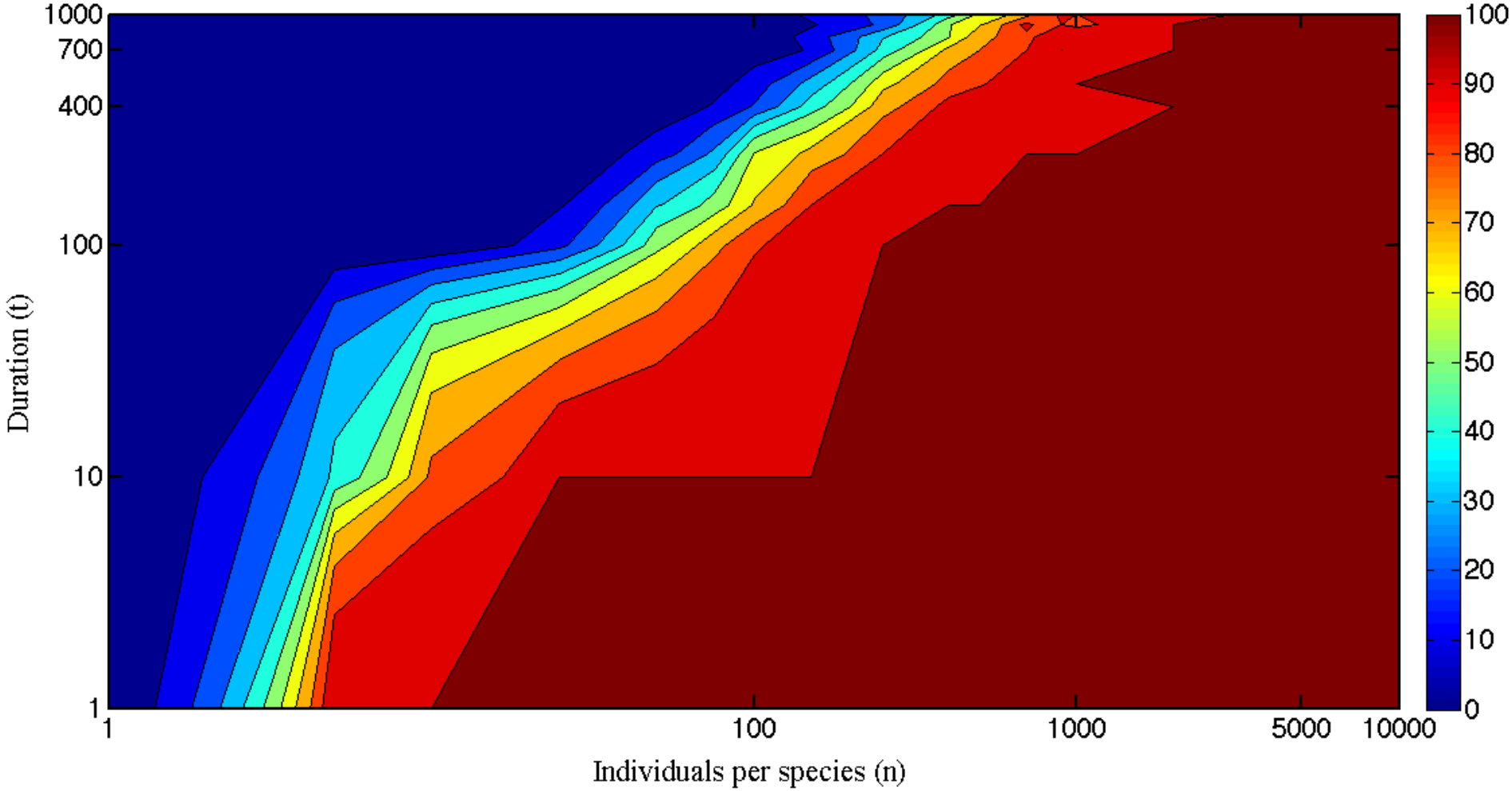
Inferior Competitor Persists



Paradox

Rowlett & Menden-Deuer, 2014

Inferior Competitor Persists



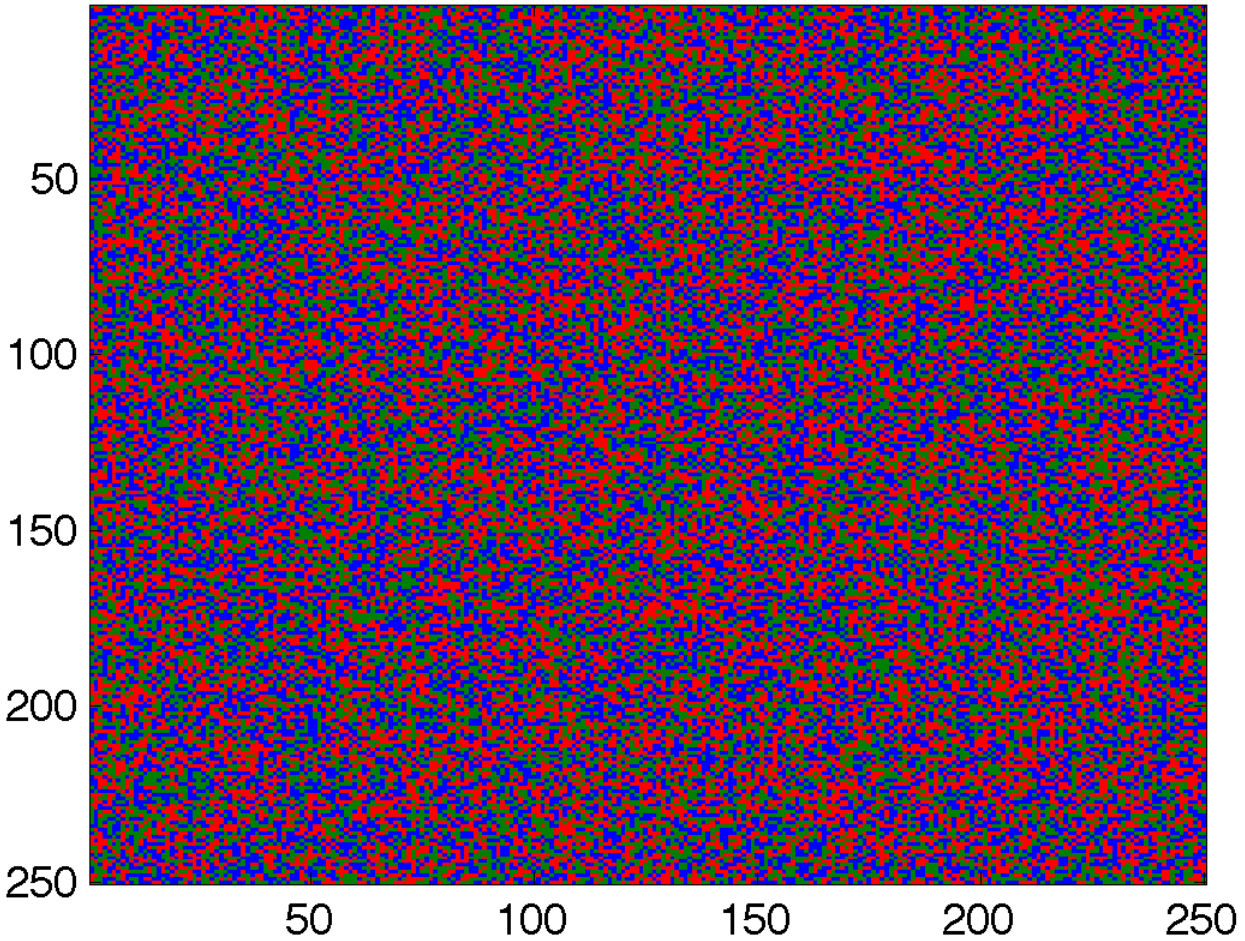
Paradox

Rowlett & Menden-Deuer, 2014

What about spatial heterogeneity?

- spatially explicit competition local vs global
- constant behavior or strategic i.e. variable

Tzero

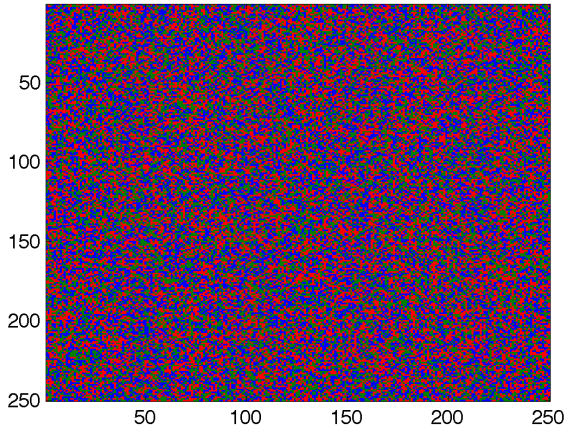


Paradox *Menden-Deuer & Rowlett, 2014*

What about spatial heterogeneity?

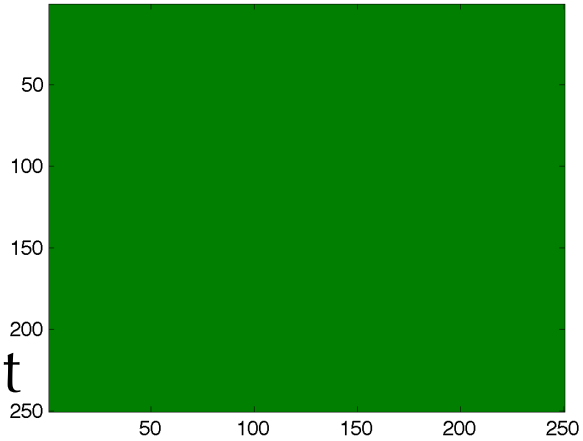
- spatially explicit competition delays extinction
- species persist when intra-specific variability is incorporated, irrespective of spatial structure

Tzero

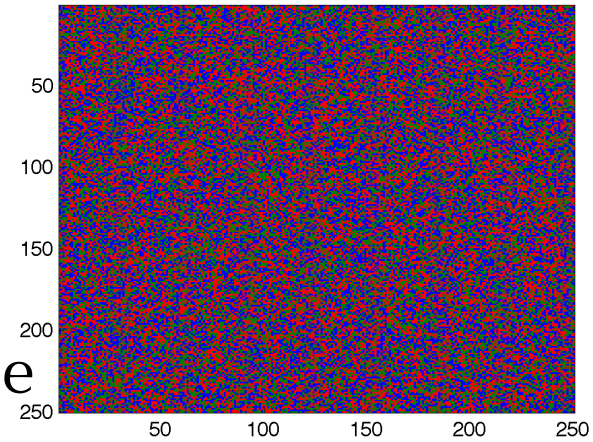


Tfinal

constant



variable

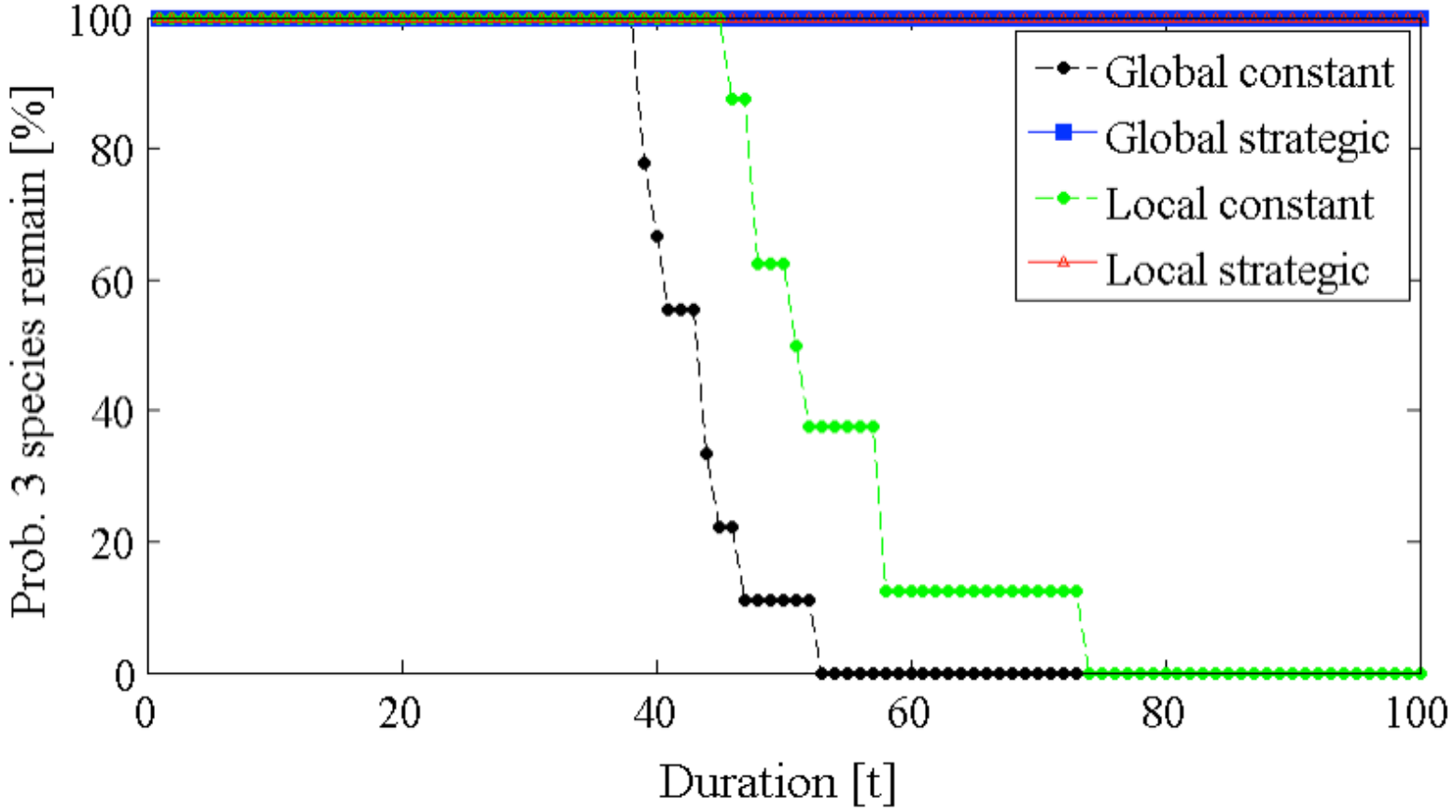


Paradox

Menden-Deuer & Rowlett, 2014

What about spatial heterogeneity?

- spatially explicit competition delays extinction
- incorporation of variability maintains species persistence, irrespective of spatial structure of competition



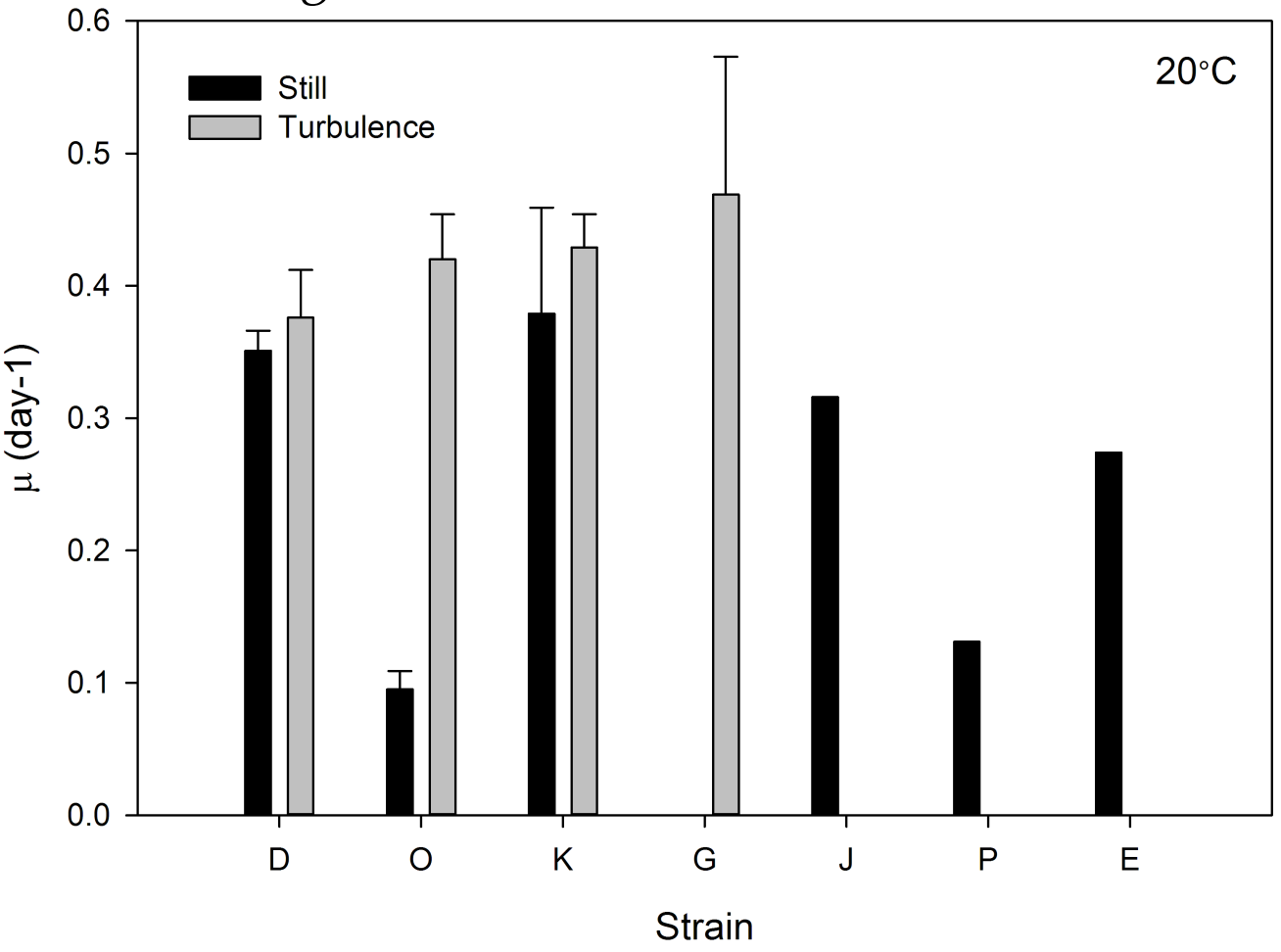
Paradox *Menden-Deuer & Rowlett, 2014*

NASA SeaWIFS 10 year average Surface Fluorescence

Paradox

Digression: some dinos love turbulence

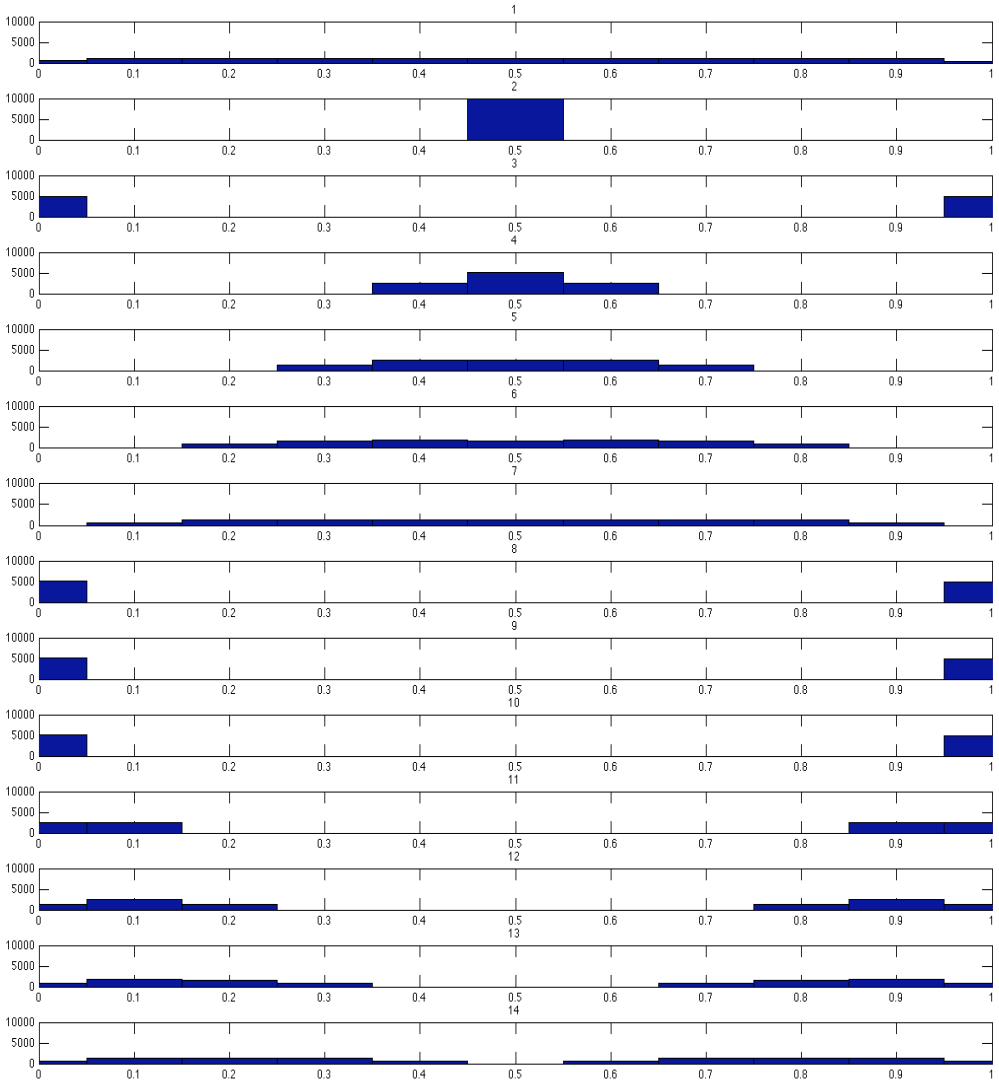
- variable growth rate across strains of same phytoplankton species *Akashiwo sanguinea*



Paradox Menden-Deuer & Montalbano 2015

Probing the role of intra-specific variability

- 14 behavior distributions
- identical mean
- increased variance
- bimodal distributions



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Menden-Deuer & Rowlett, in prep.

Probing the role of intra-specific variability

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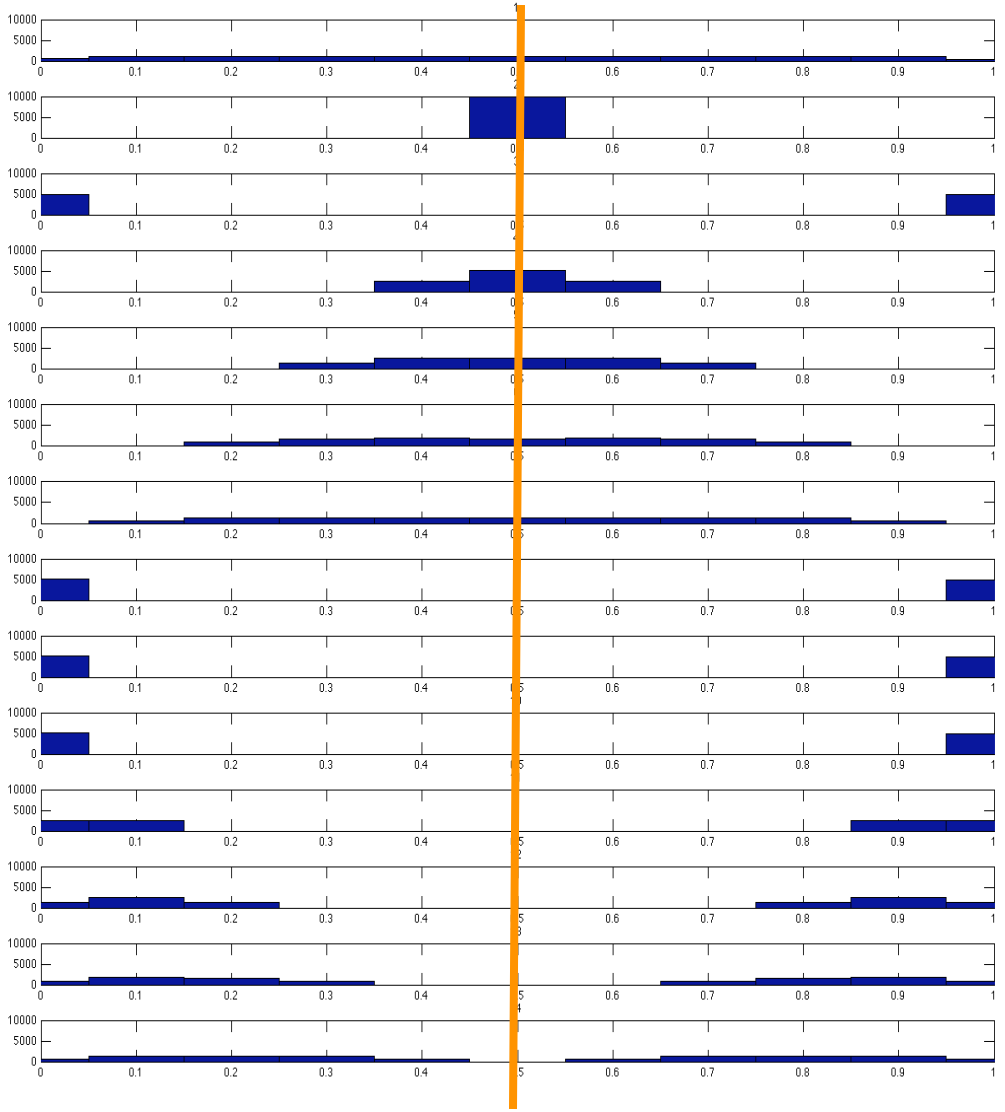
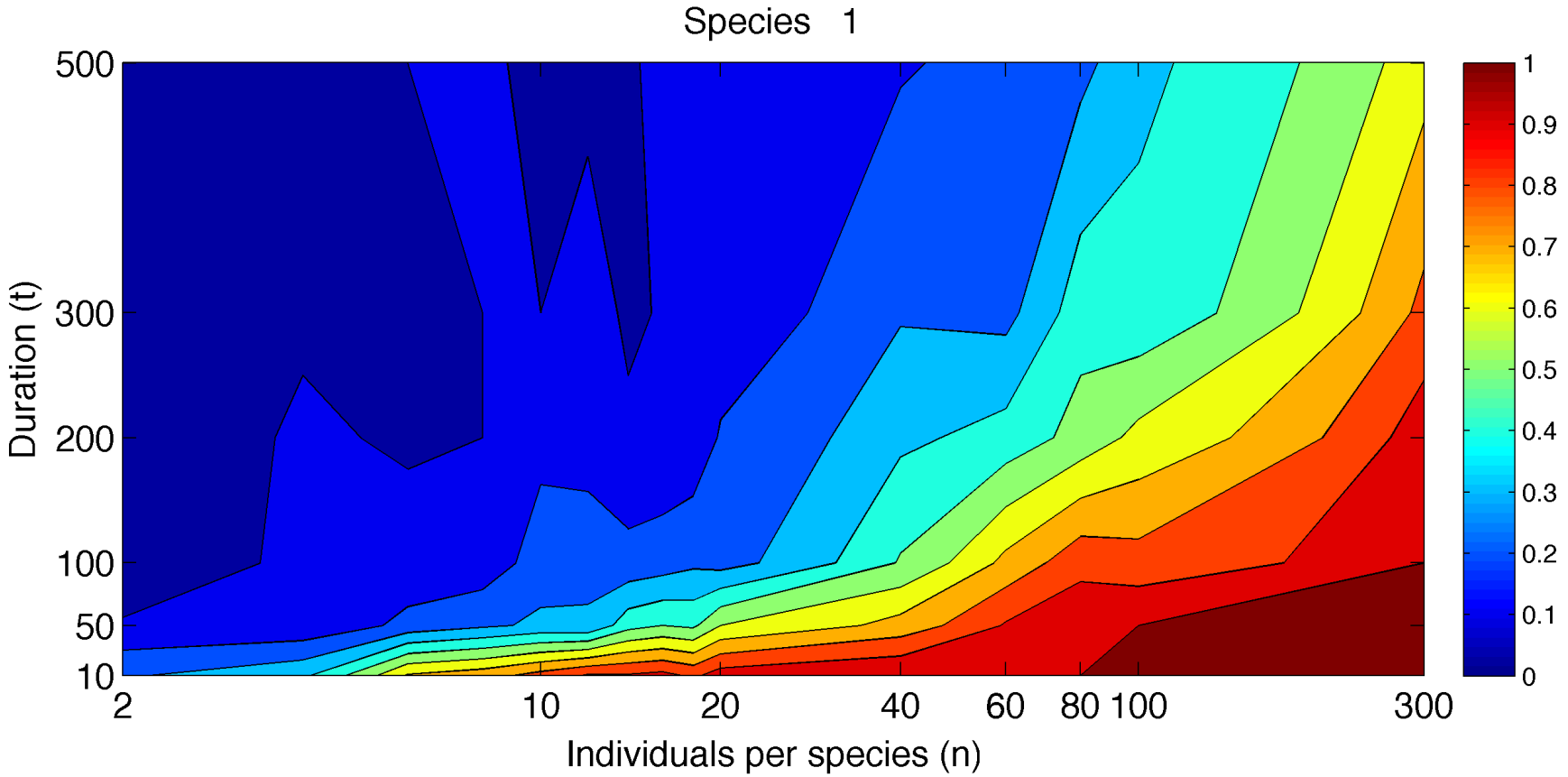


Paradox

Menden-Deuer & Rowlett, in prep.

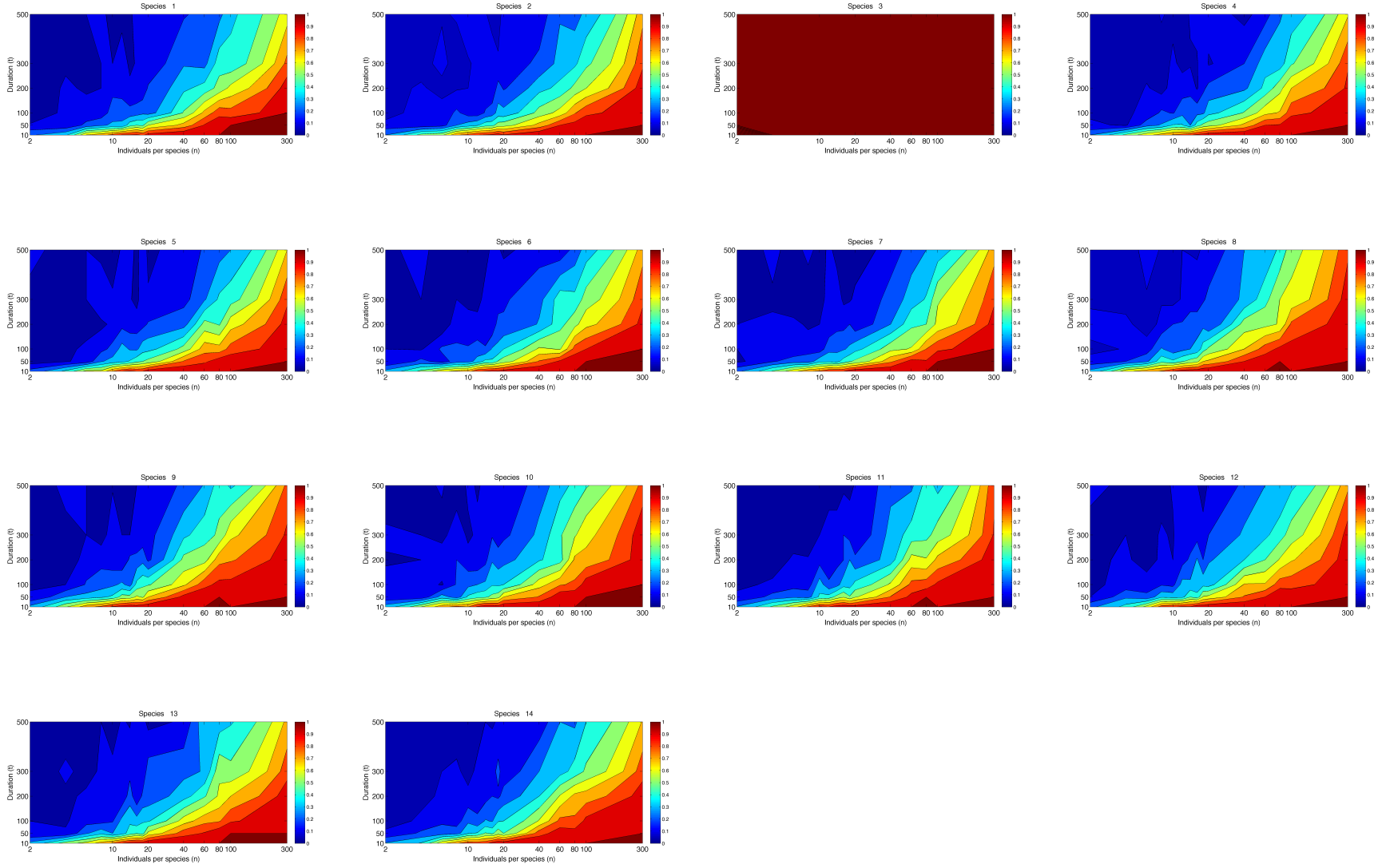
Survival probability

- for each behavior/competitive ability distribution
- survival probability in 100 replicated competitions simulations
- variation in population size and duration



Paradox *Menden-Deuer & Rowlett, in prep.*

No penalty for type of variability distribution

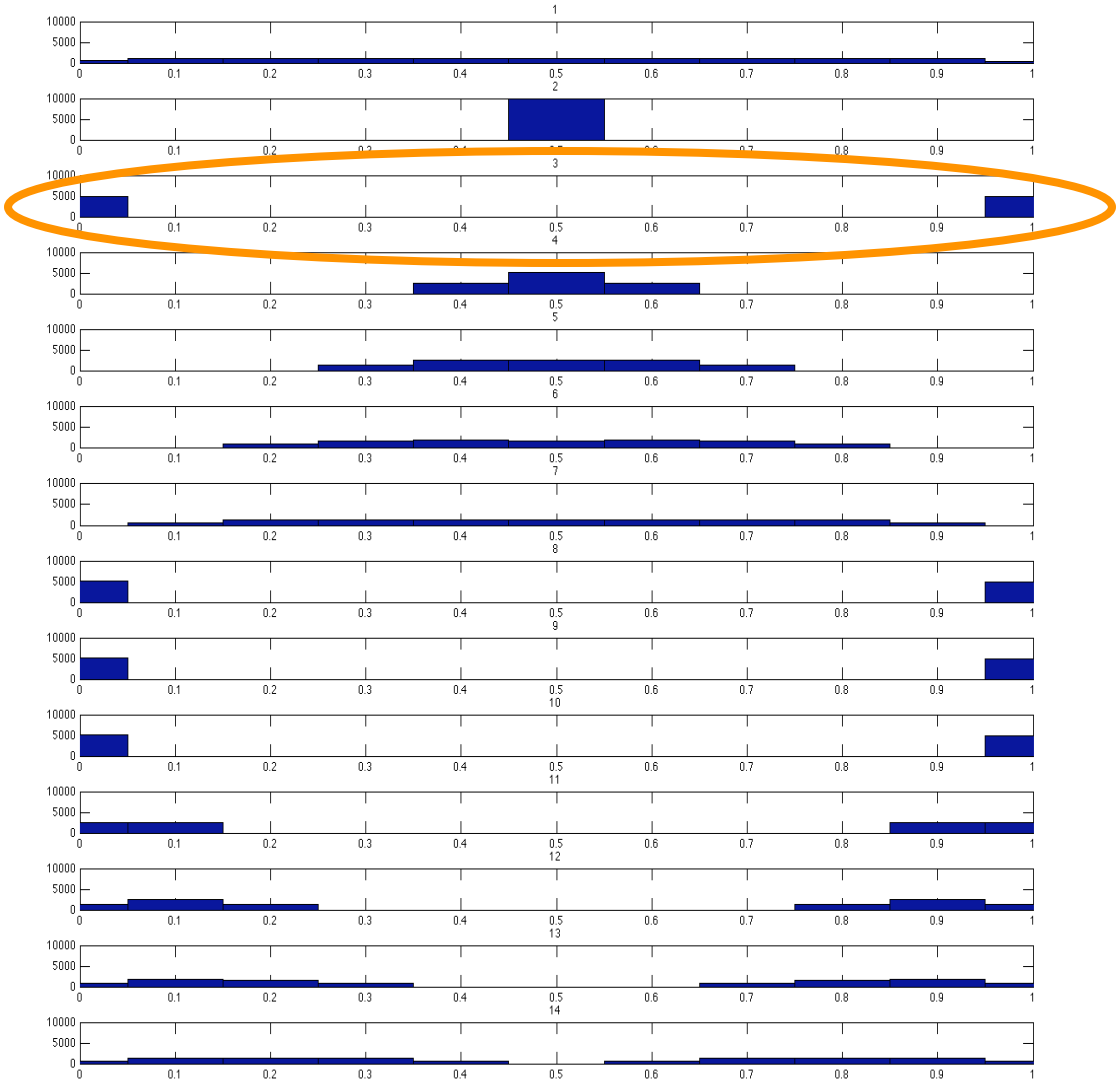


Paradox

Menden-Deuer & Rowlett, in prep.

Probing the role of intra-specific variability

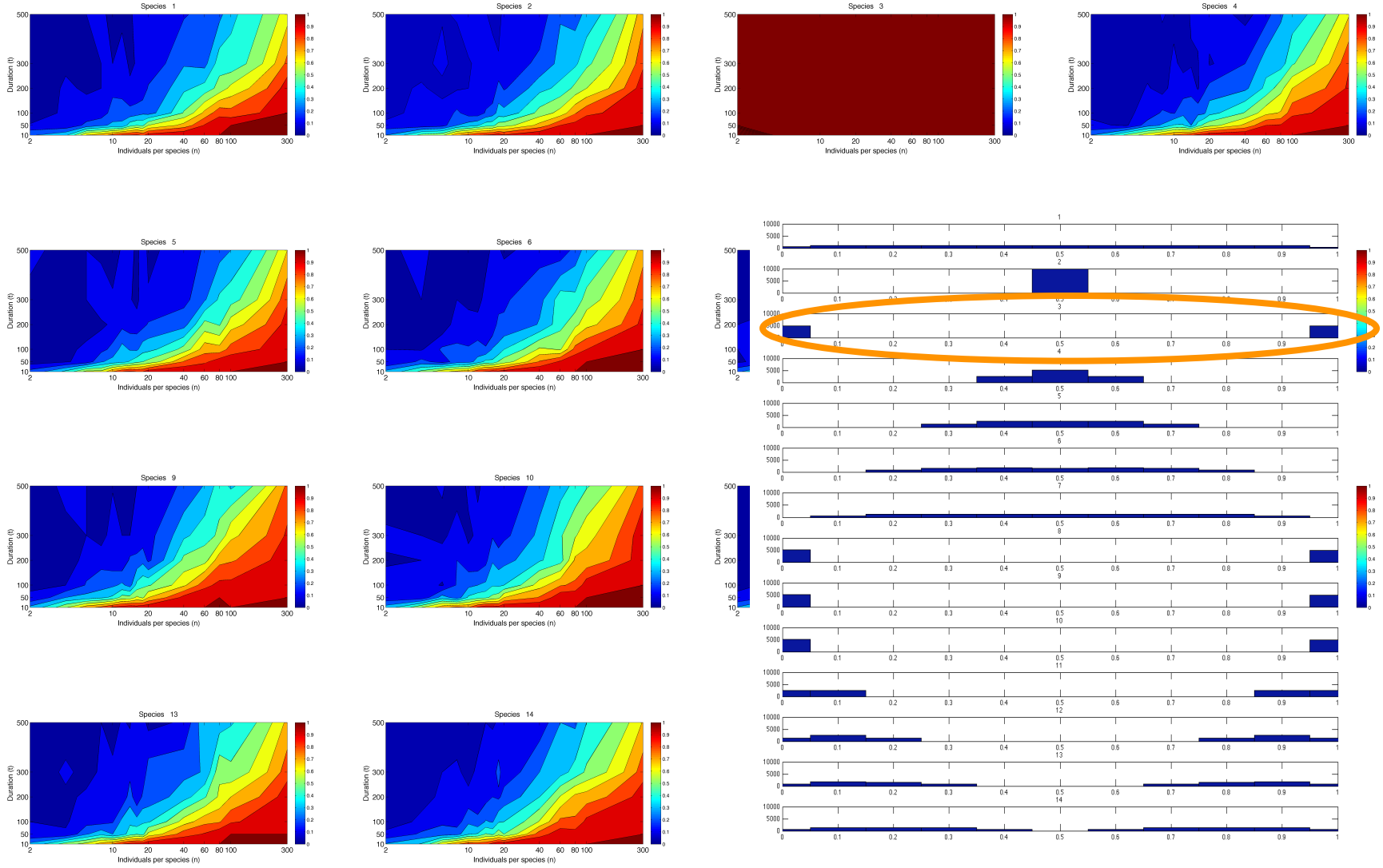
- 14 behavior distributions
- identical mean
- increased variance
- bimodal distributions



Paradox

Menden-Deuer & Rowlett, in prep.

Hyper-variability = invulnerable?



Paradox

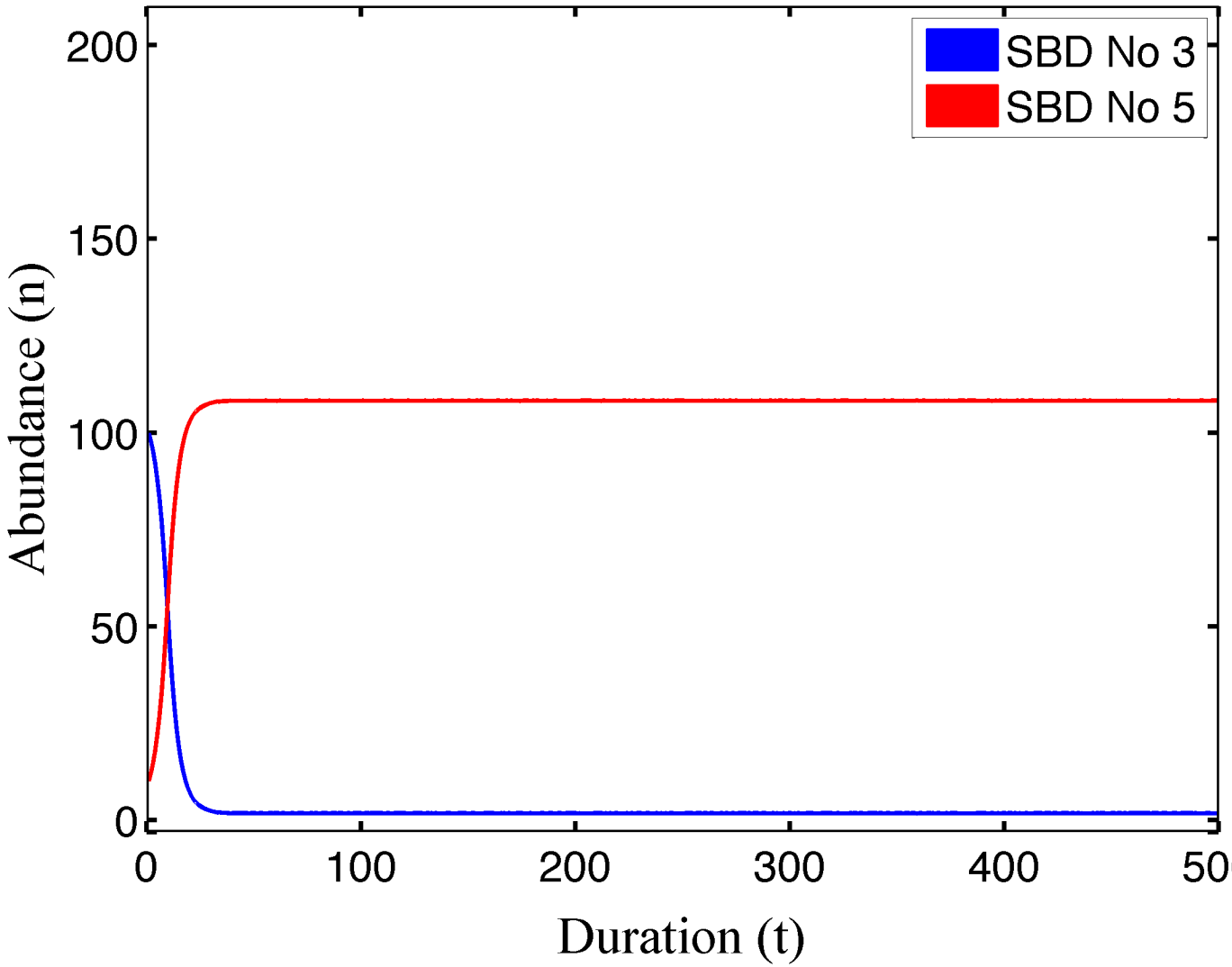
Menden-Deuer & Rowlett, in prep.

Bimodal distribution is a survival champion

- *even at smaller starting distributions*

Bimodal distribution is a survival champion

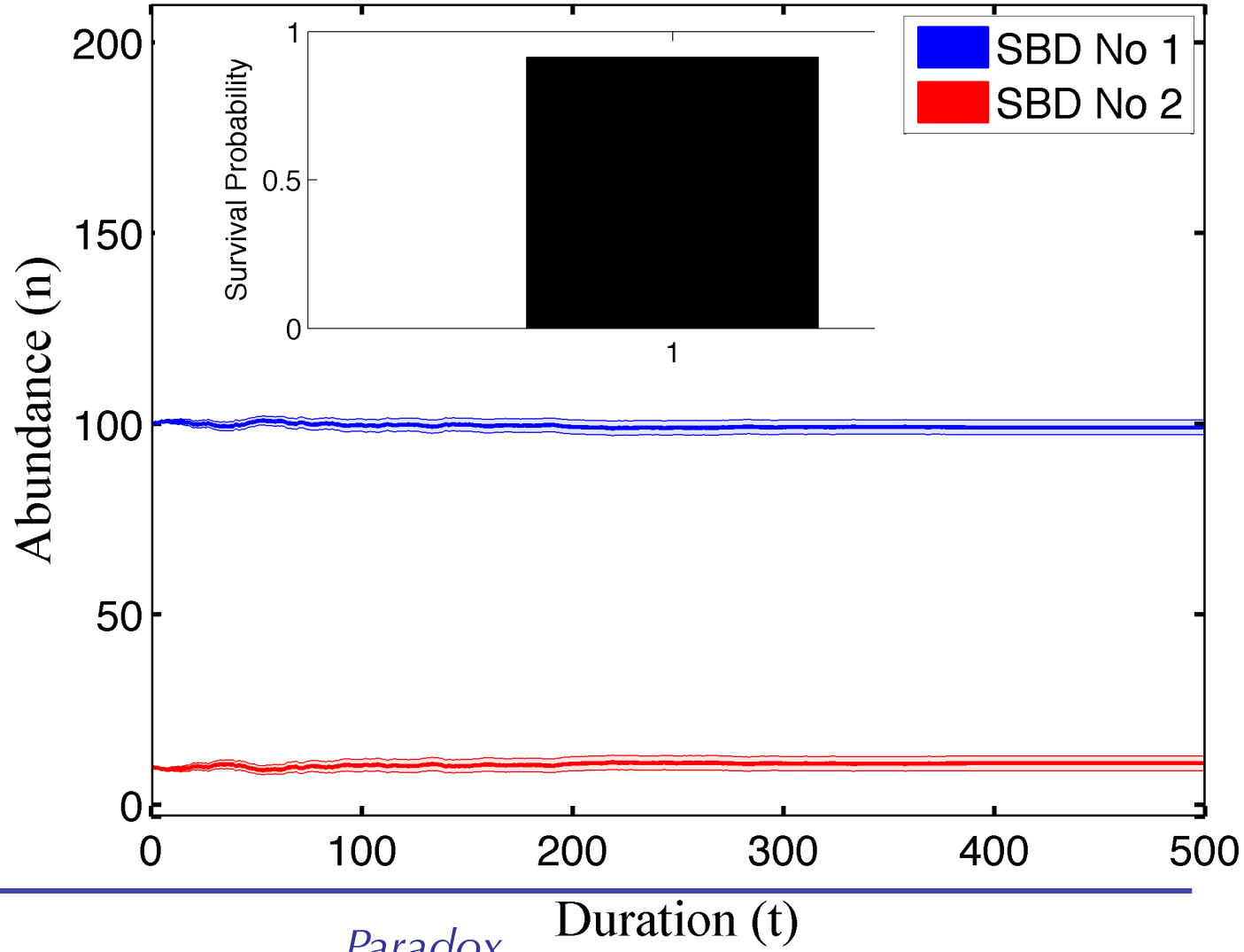
- *but not invasion*



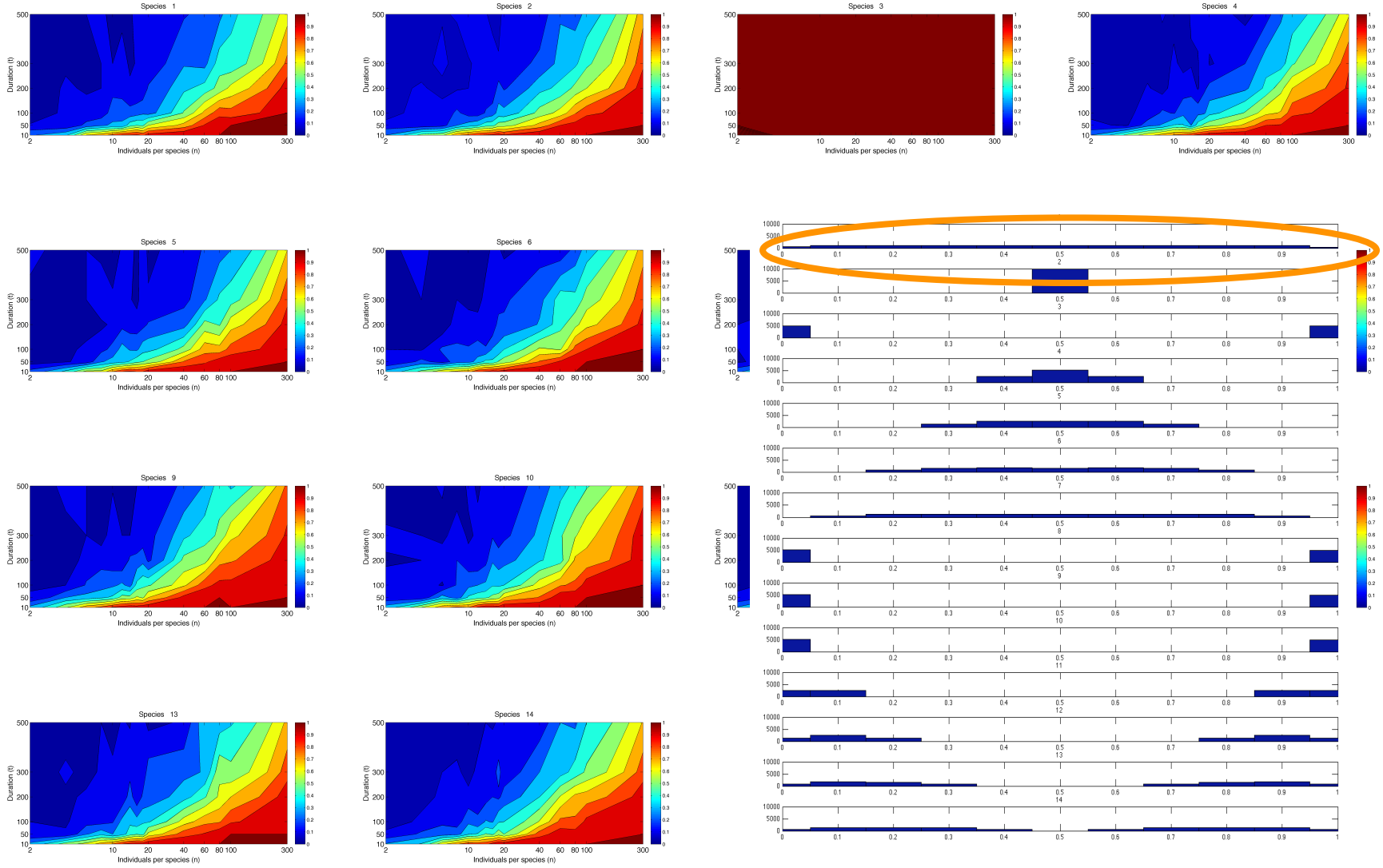
Paradox

Hyper-variable distribution withstands invasi

- populations with a maximally variable distribution are resistant against invasion from invariant ones



Hyper-variable rules? Invasion resistance



Paradox

Menden-Deuer & Rowlett, in prep.

Hyper-variability = non-invadable