# Ecological structure and function in variable environments

Carling Bieg

October 28, 2024 • Paris, France

University of Guelph · Yale · Case Western Reserve University

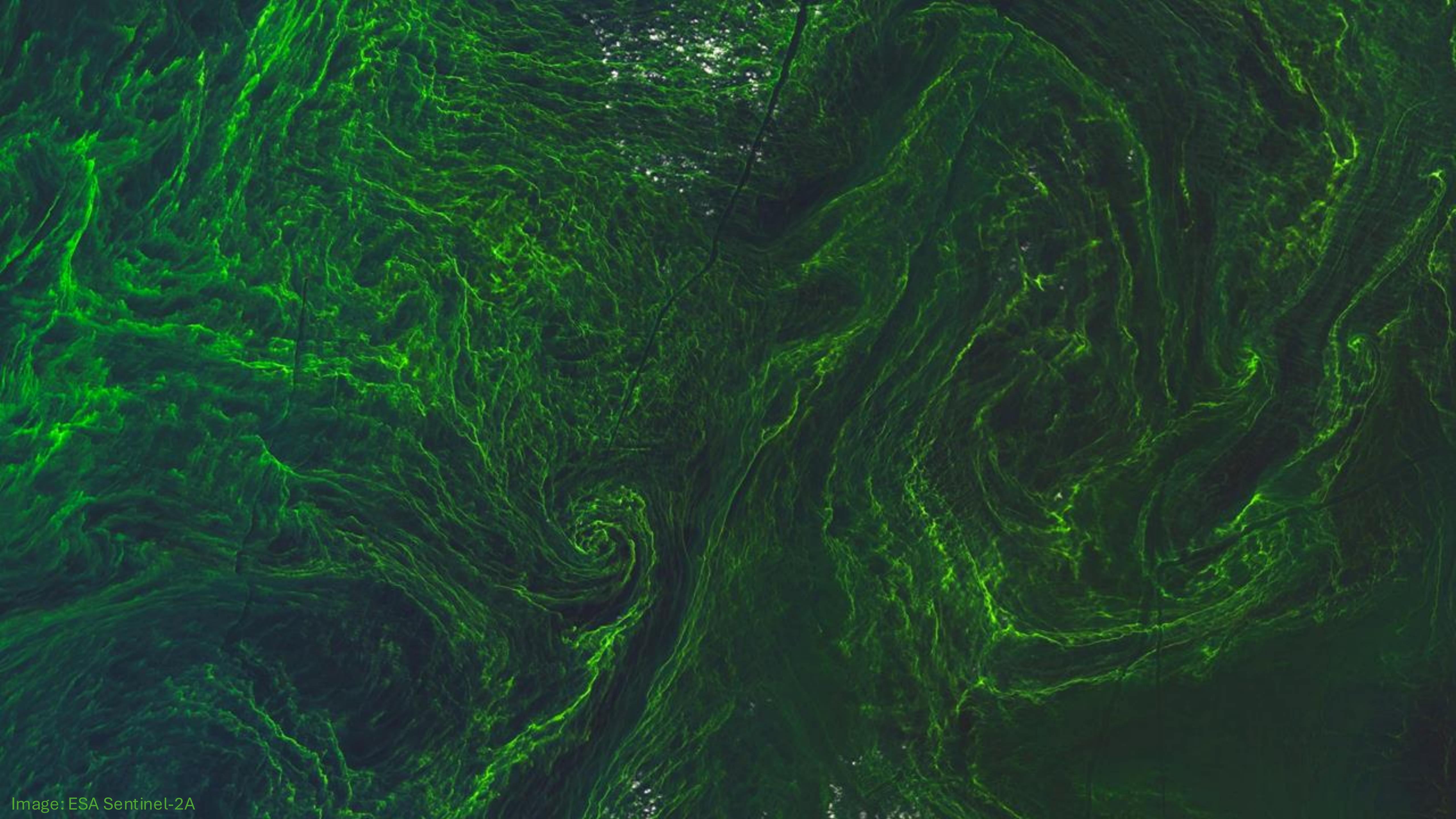


Image: ESA Sentinel-2A

# Cambodia's "Beating Heart"

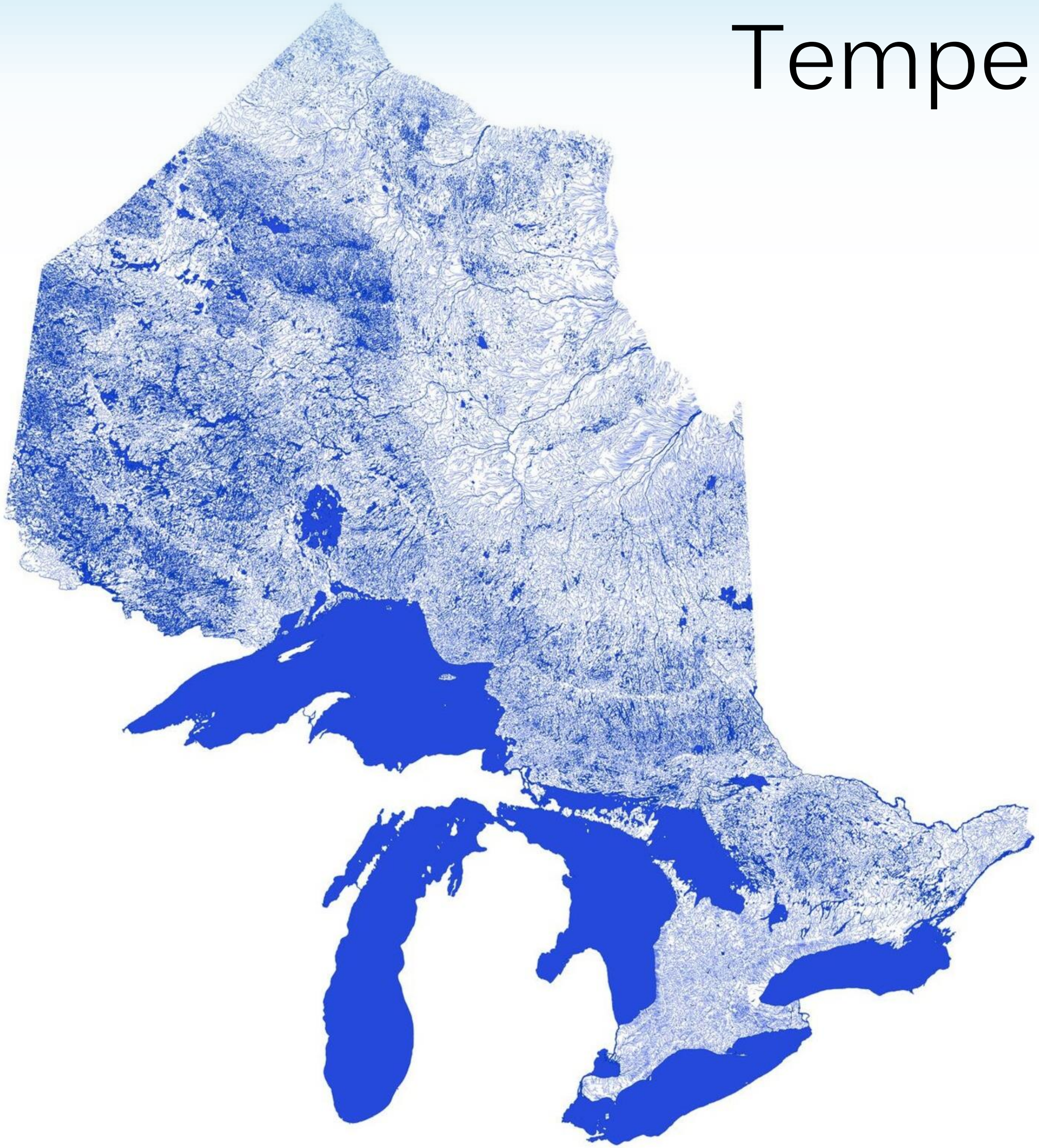
Video: Allan Michaud | YouTube


Image: Marcelo Kraus

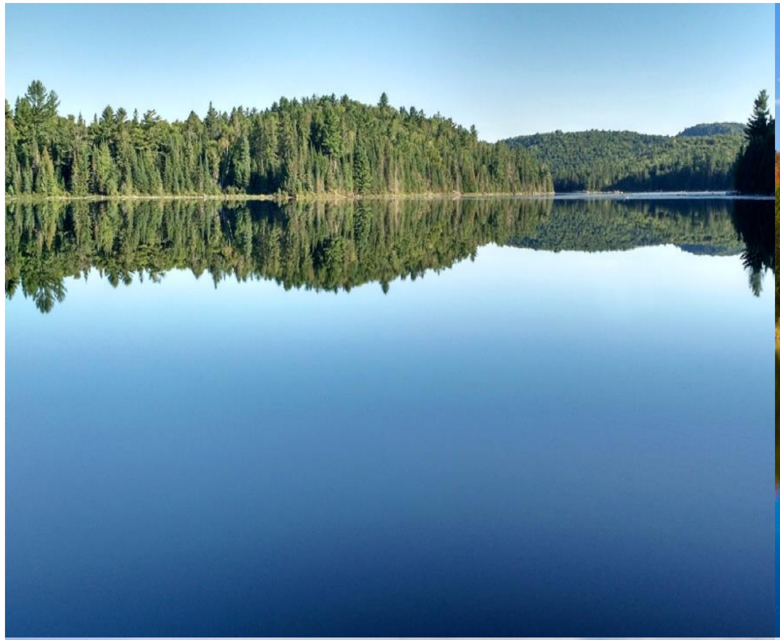
Image: Alamy

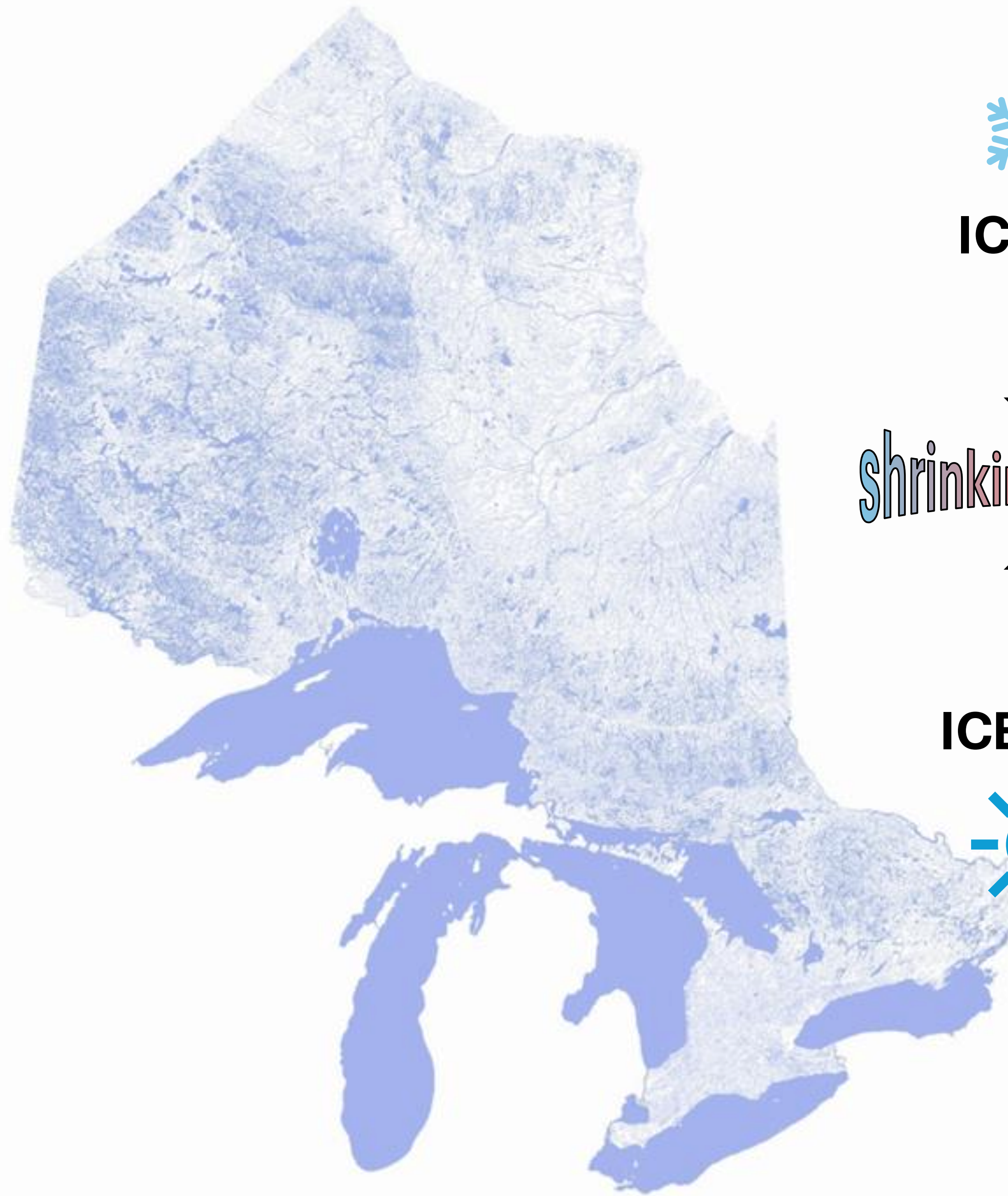

**"Death by a thousand cuts"**

# Temperate Lakes



# Temperate Lakes

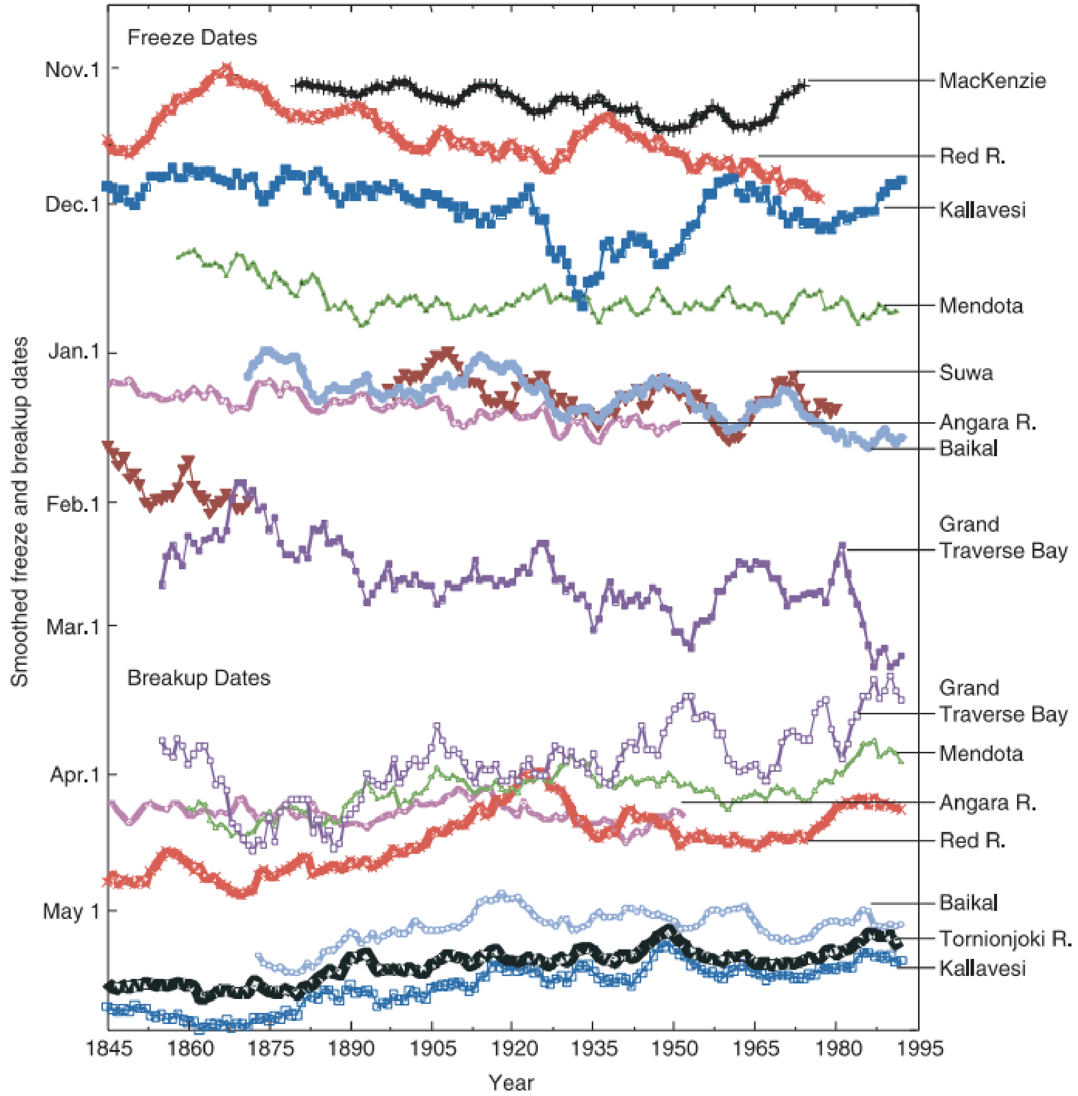




ICE ON

shrinking winters

ICE OFF




**Historical Trends in Lake and River Ice Cover in the Northern Hemisphere**


John J. Magnuson,[1]* Dale M. Robertson,[2] Barbara J. Benson,[1] Randolph H. Wynne,[3] David M. Livingstone,[4] Tadashi Arai,[5] Raymond A. Assel,[6] Roger G. Barry,[7] Virginia Card,[8] Esko Kuusisto,[9] Nick G. Granin,[10] Terry D. Prowse,[11] Kenton M. Stewart,[12] Valery S. Vuglinski[13]



SCIENCE VOL 289 8 SEPTEMBER 2000

# Global change is altering “nature’s heartbeat”

## Changes in environmental variation

- Seasons altered asymmetrically and becoming less extreme
- Previously smooth seasonal pulses are becoming more variable
- More extreme weather events

## & changing ecological structure and functioning

- Altered yearly patterns in primary productivity
    - Changes in energy flux fueling whole food webs
- Changes in accessible & available habitat
    - Changes in behaviour & space use
    - Altered intra- and interspecific interactions

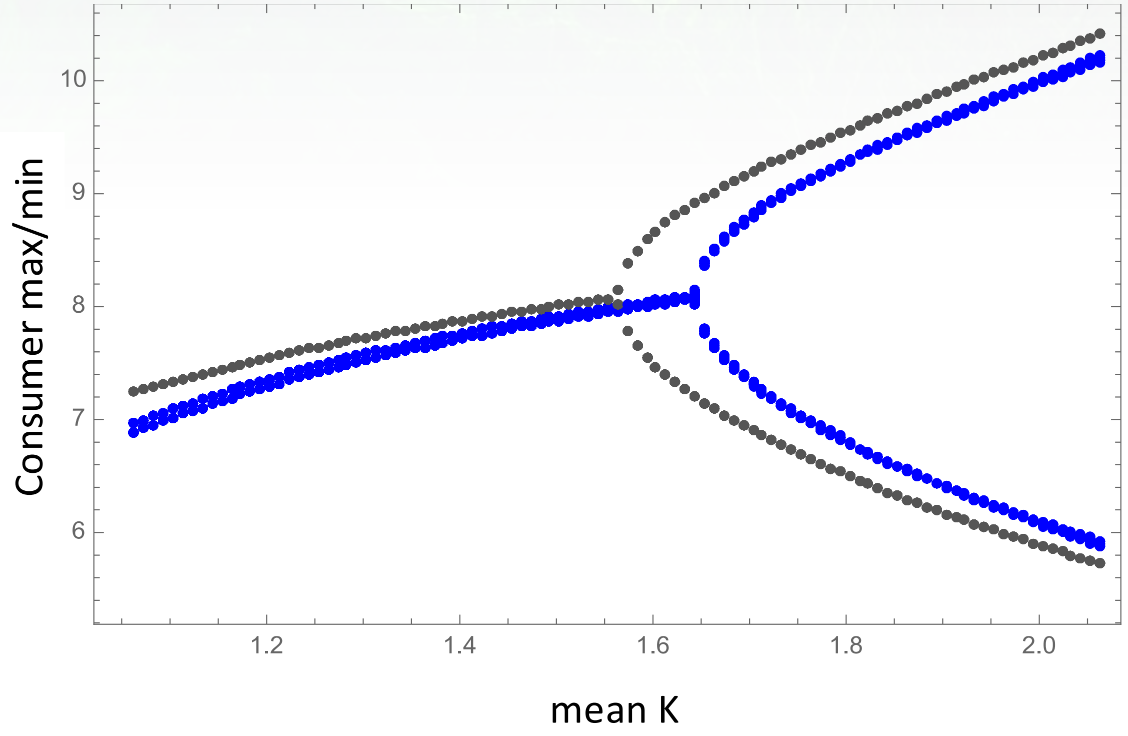
# How do fluctuations in the environment affect the structure and function of ecological systems?

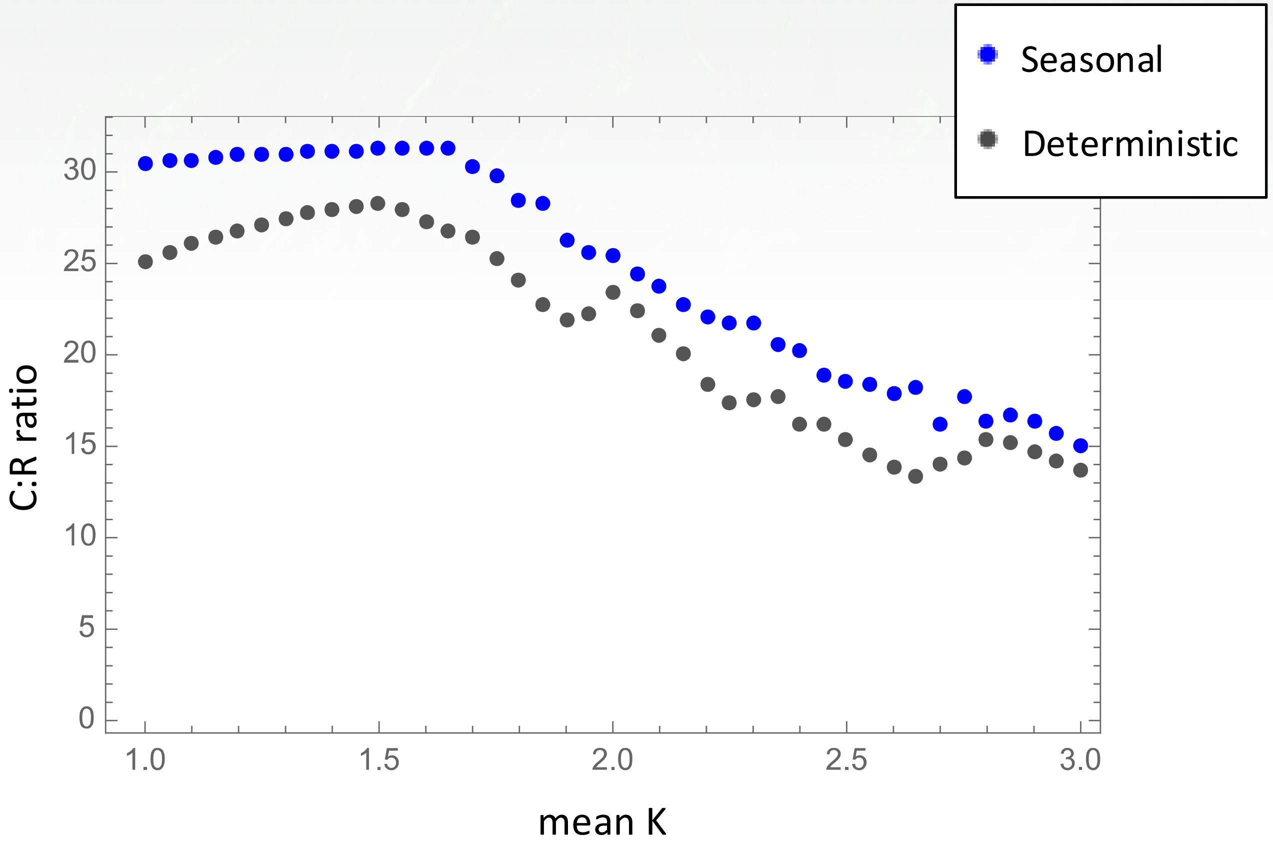
& what will changes in these natural rhythms mean for biodiversity?

# The structure & function of ecological interactions in variable environments

In consumer-resource (C-R) interactions with fluctuating productivity (K), seasonality promotes secondary production while maintaining stability.

- Seasonal forcing delays & dampens the onset of limit cycles driven by increasing K.
- Allows for more C biomass per unit of R.




Bieg et al. 2024 *Proceedings B*

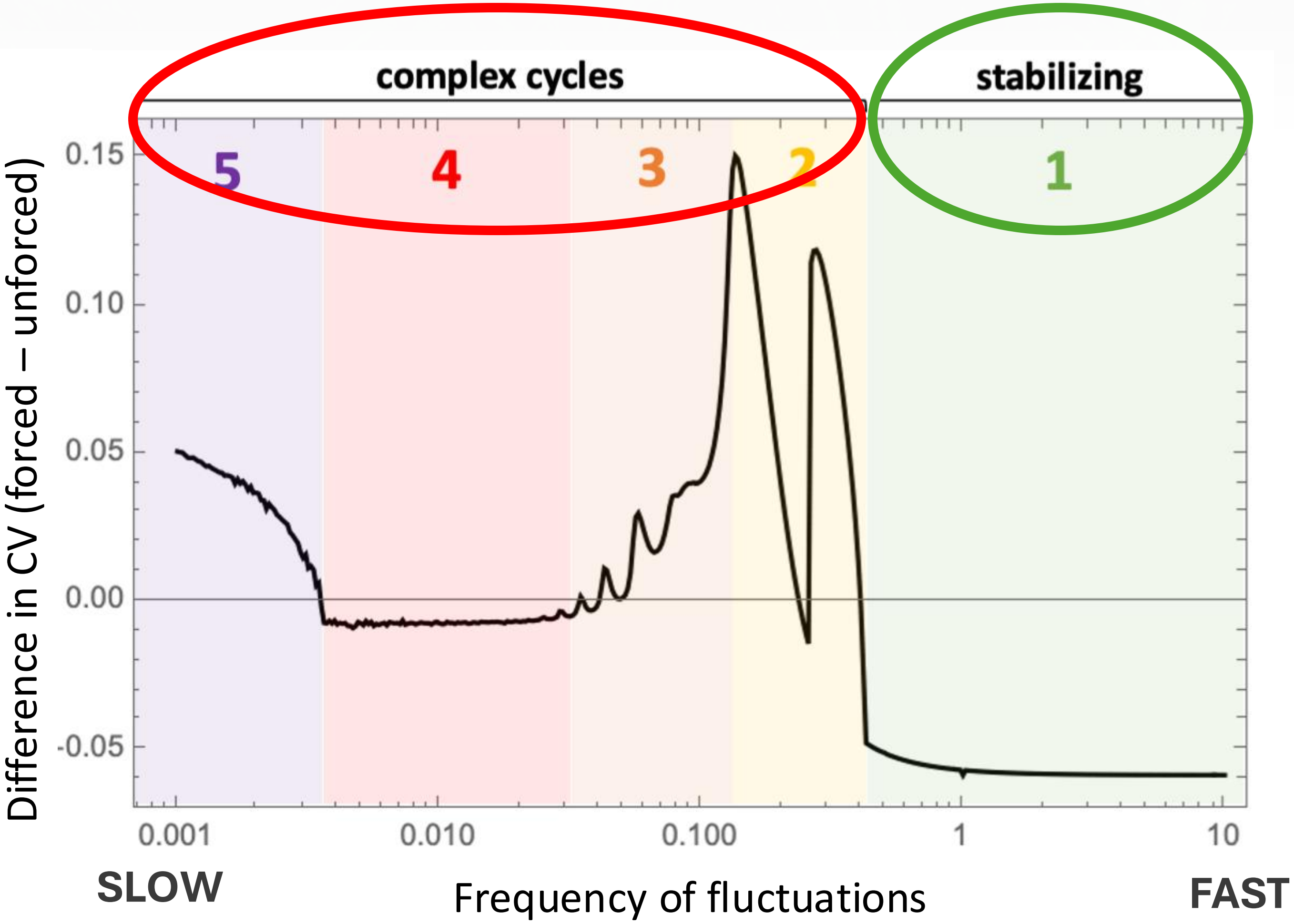
# The structure & function of ecological interactions in variable environments

In consumer-resource interactions with fluctuating productivity (K),

- Fast fluctuations are stabilizing
- Slow fluctuations drive complex cycles

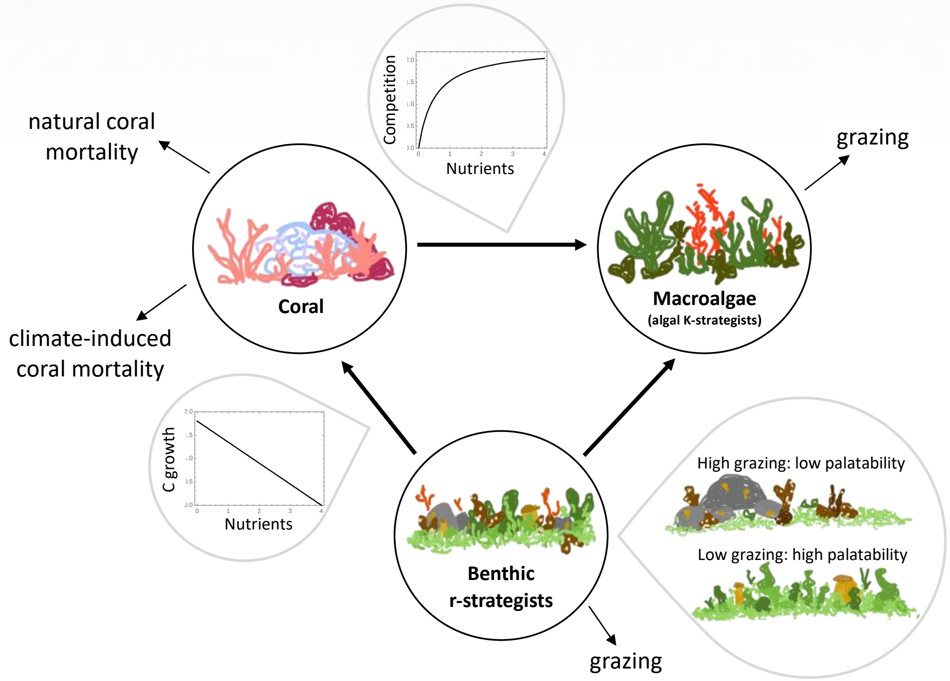
Environmental fluctuations & biotic dynamics have a complex interaction.

- Result depends on *relative* time scales of intrinsic vs. extrinsic oscillators.
- Dynamics are driven by a combination of **local** & **non-local** properties.

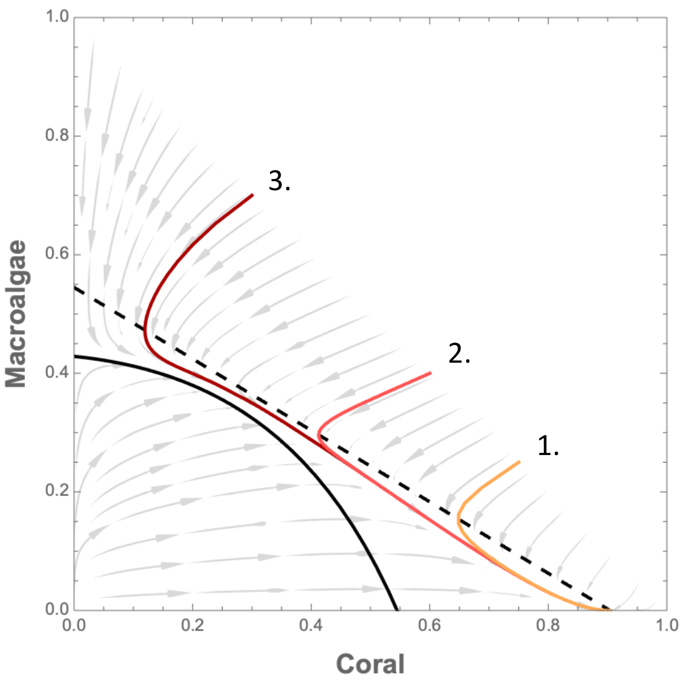



Bieg et al. 2024 *Proceedings B*

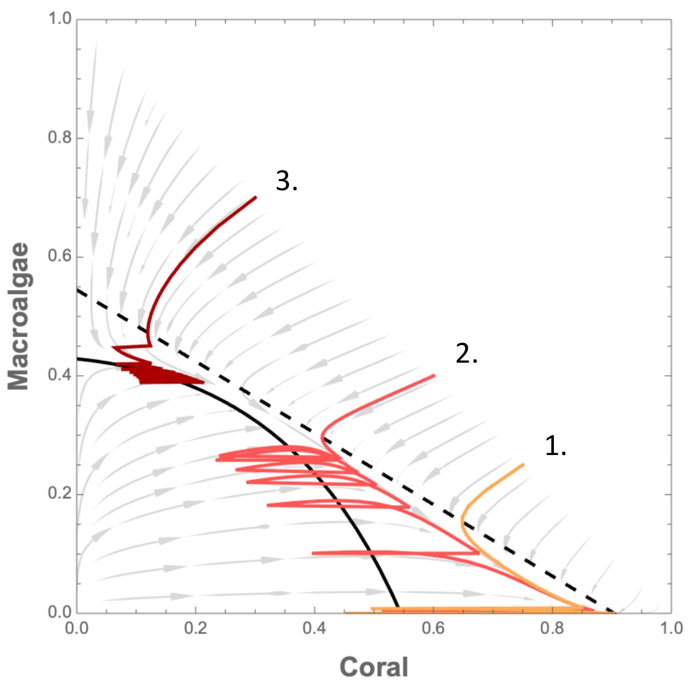
# In coral reefs, repeated disturbances drive quasi-stable noise-driven alternate states not predicted from deterministic skeleton




## Deterministic trajectories




## Flow-kick trajectories




— Macroalgae isocline  - - - Coral isocline

Bieg et al. 2024 *Ecosystems*

The interaction between environmental noise and ecological structure (i.e., local and nonlocal properties, relative rates of change) determine a system's response to environmental variation.

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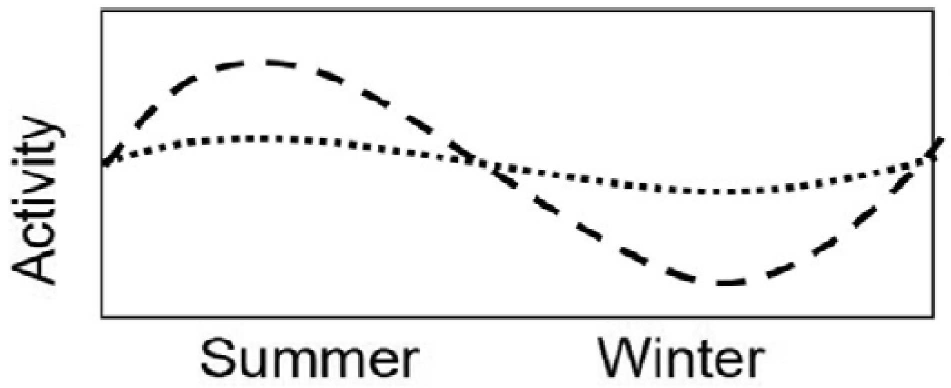
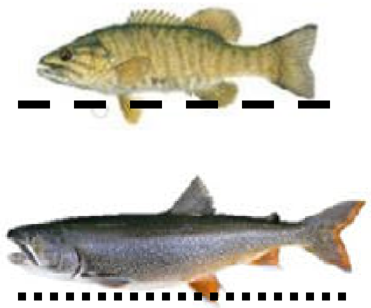
There remains a need to understand how different interaction structures respond to changing noise conditions, especially when multiple parameters respond to the environment simultaneously.

# Coexistence in Periodic Environments

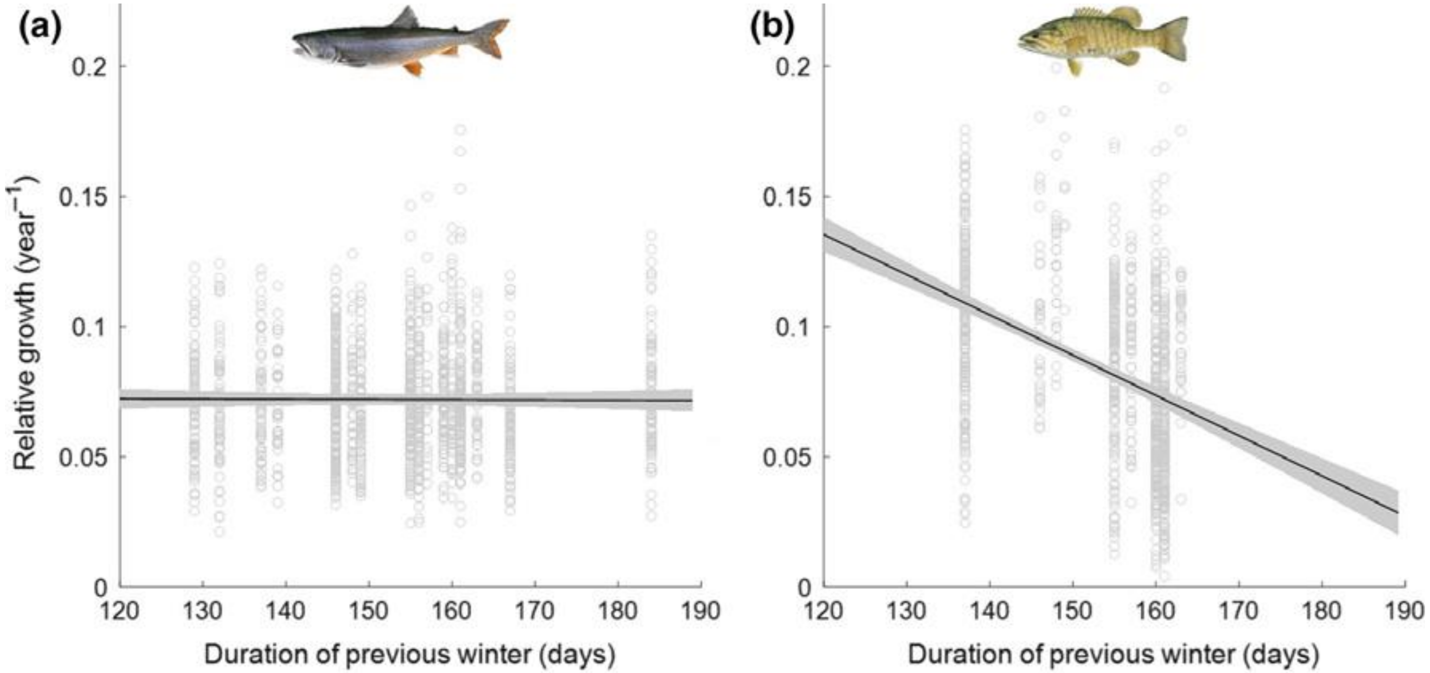



**Biological motivation:**
competing species with differential thermal preferences, seasonal behavioural patterns & relative seasonal performance



Warm-adapted species

Cold-adapted species





ECOLOGY LETTERS

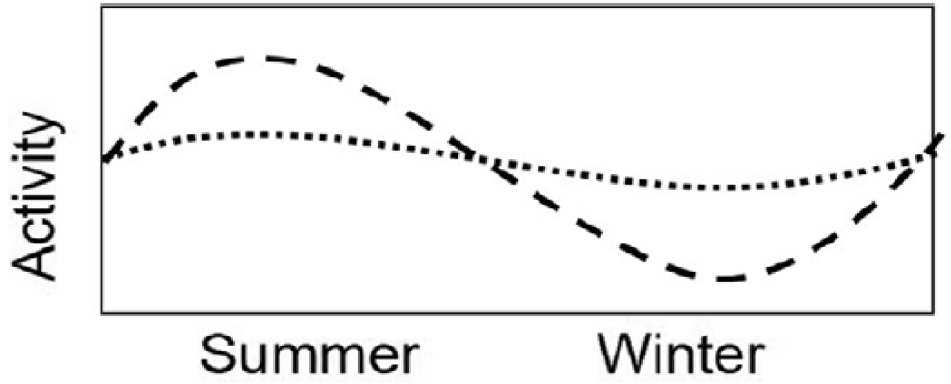
Ecology Letters, (2020) doi: 10.1111/ele.13504

IDEAS AND PERSPECTIVES

Winter in water: differential responses and the maintenance of biodiversity

McMeans et al. 2020

# Coexistence in Periodic Environments




**Biological motivation:**
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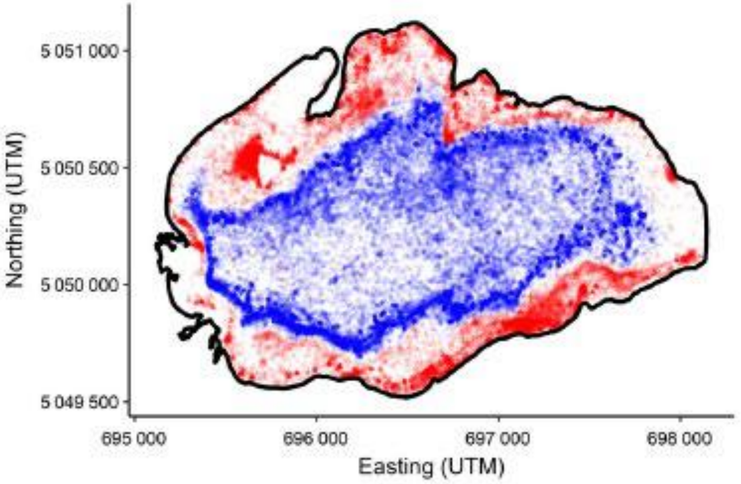
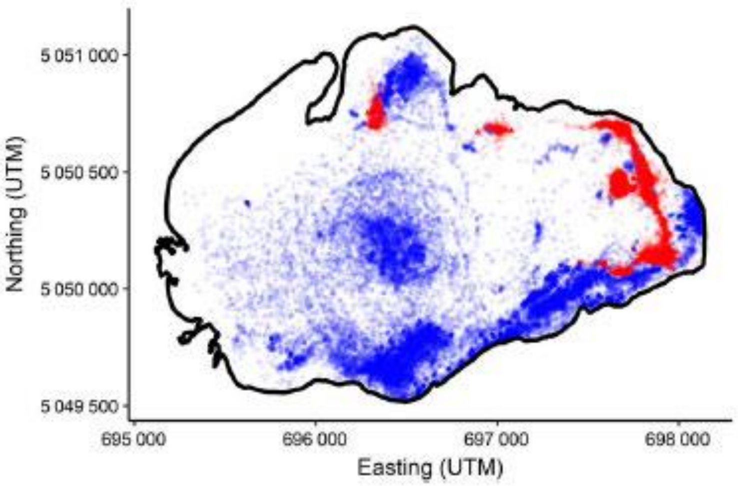
Warm-adapted species

Cold-adapted species

Seasonal Habitat Use





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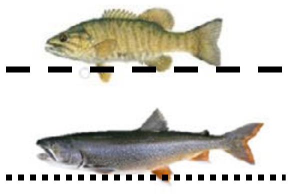
# Coexistence in Periodic Environments

Two alternating "periods" for which competing species are differentially adapted

**Model:**

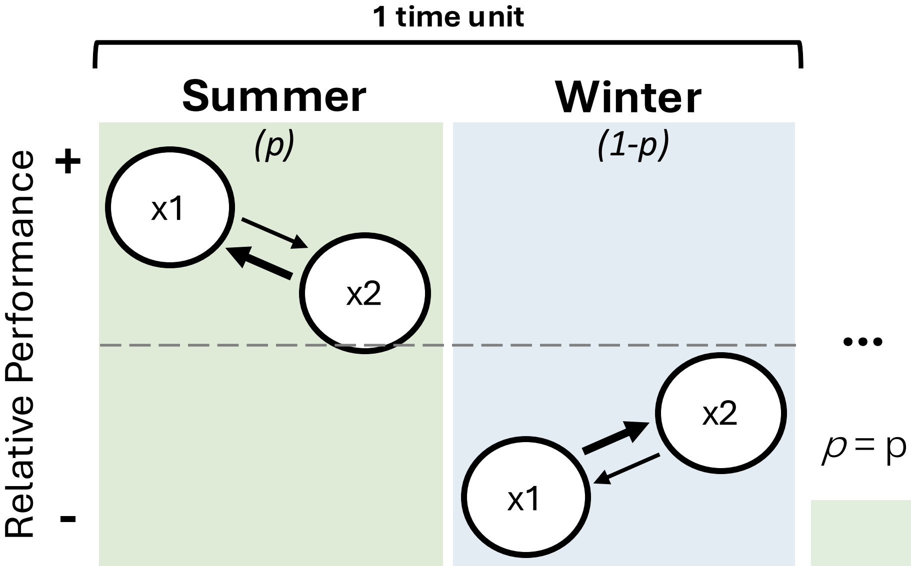
- Competing species with temporal trade-offs
- Step function iterated between seasonal conditions (i.e., parameters change seasonally)

**Experiment:** Changing proportion of time under different seasonal conditions ($p$)



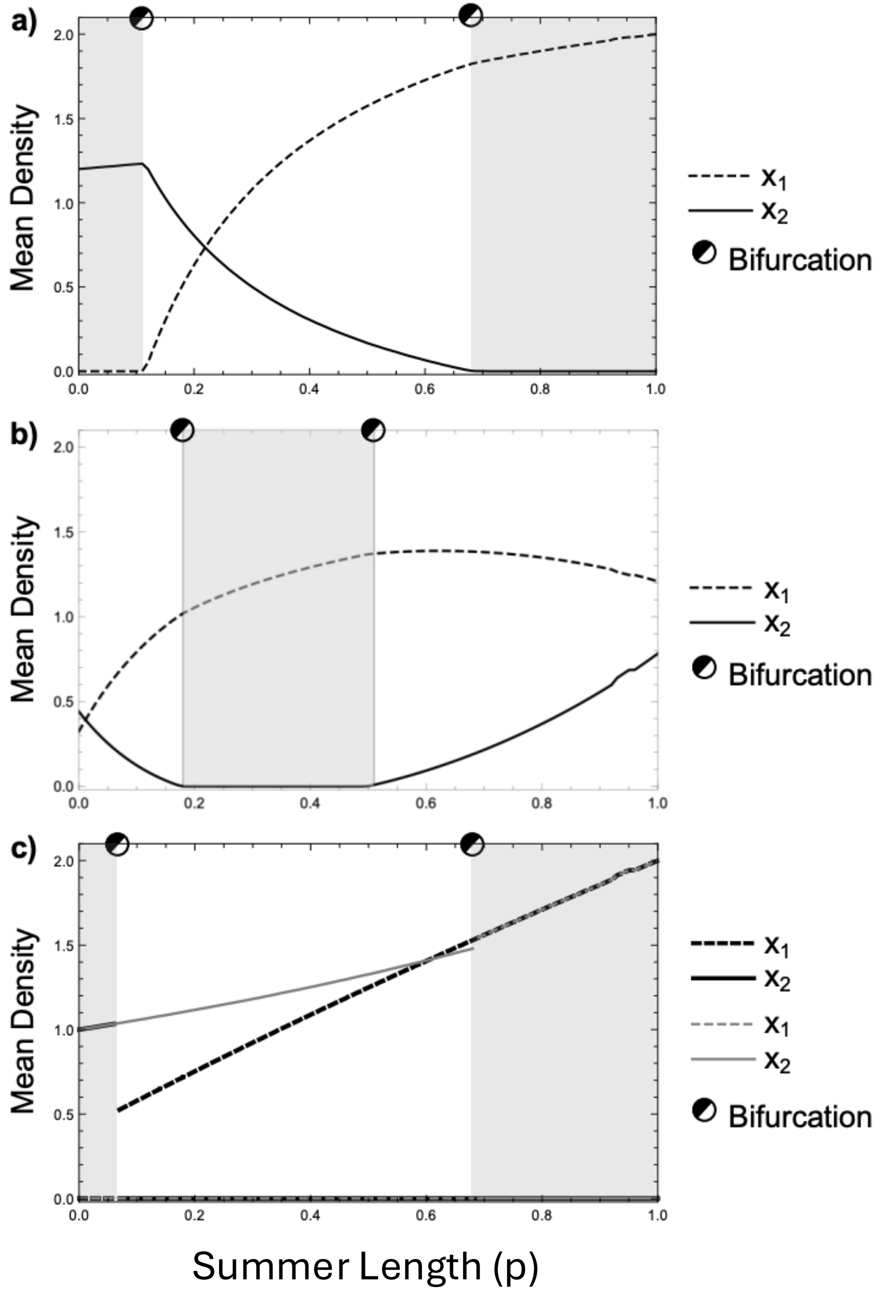

$$\frac{dX_{j,\varphi}}{dt} = r_{\varphi,j}X_j(1 - \alpha_{\varphi,jj}X_j - \alpha_{\varphi,jk}X_k)$$

$\varphi$ = season (s or w)




$p$ = proportion of year that is summer

# Seasonally-mediated coexistence outcomes




**Seasonally-mediated coexistence**

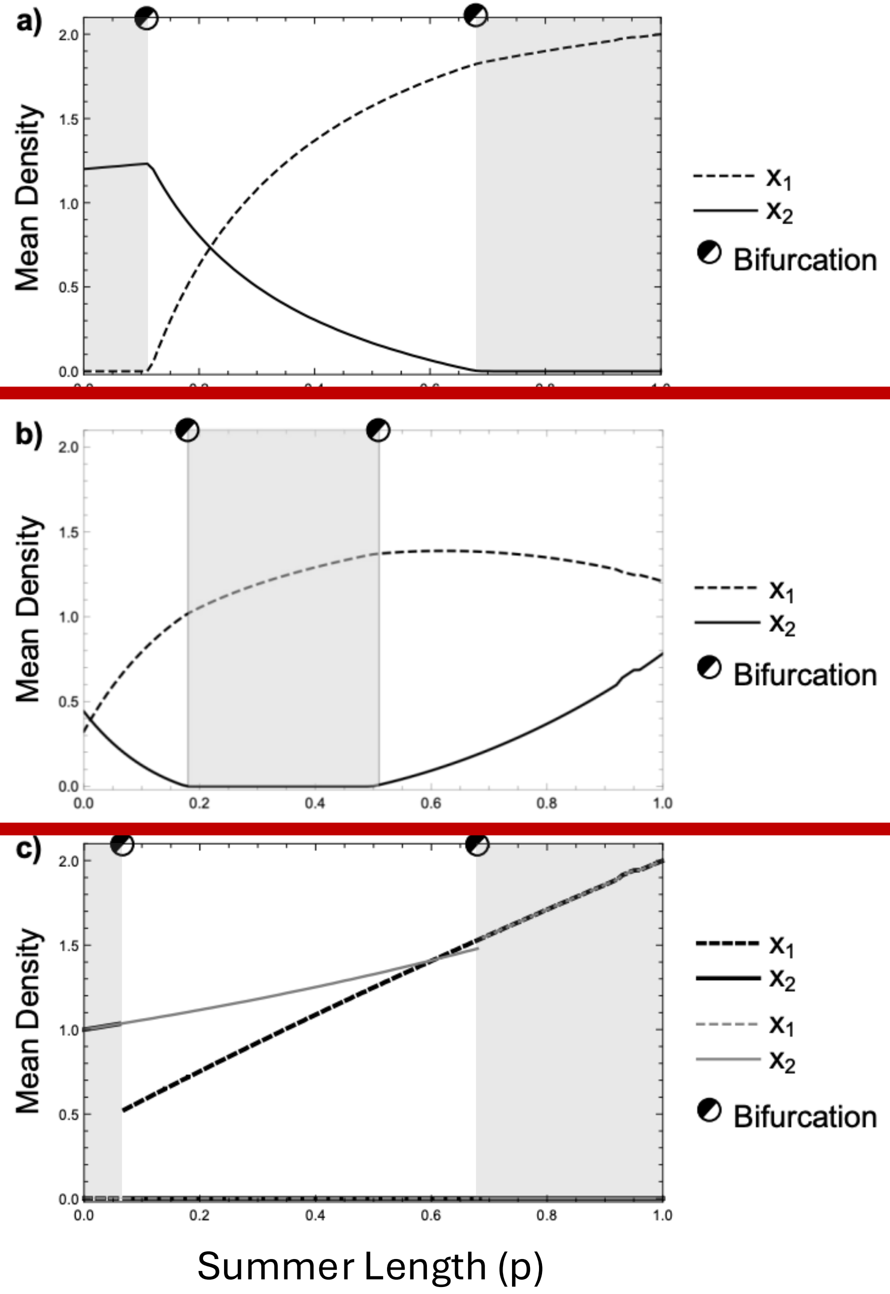
**Seasonally-mediated competitive exclusion**

**Seasonally-mediated contingent coexistence**

Alexa Scott

McMeans et al. (2020) *Eco Letts*; Scott et al. *Biorxiv* DOI:10.1101/2023.02.24.529749

# Seasonally-mediated coexistence outcomes




**Seasonally-mediated coexistence**

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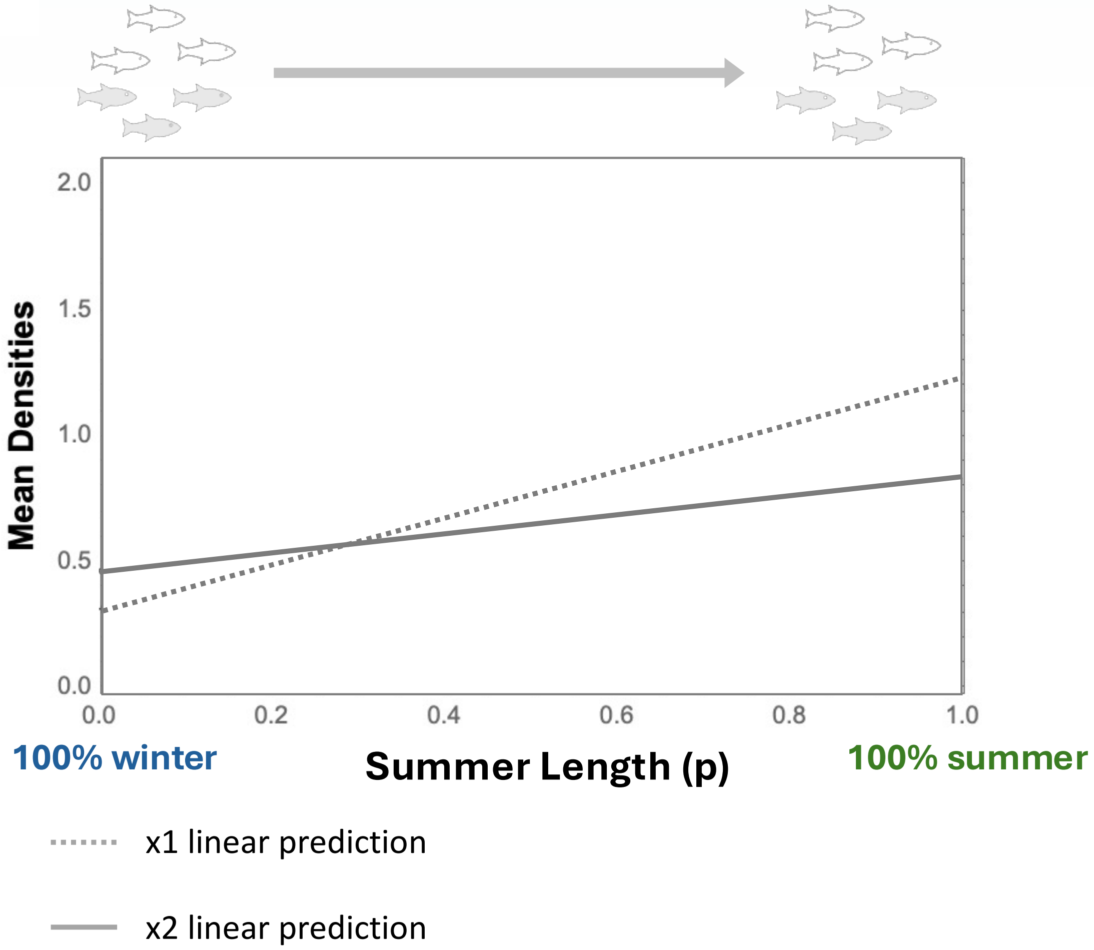
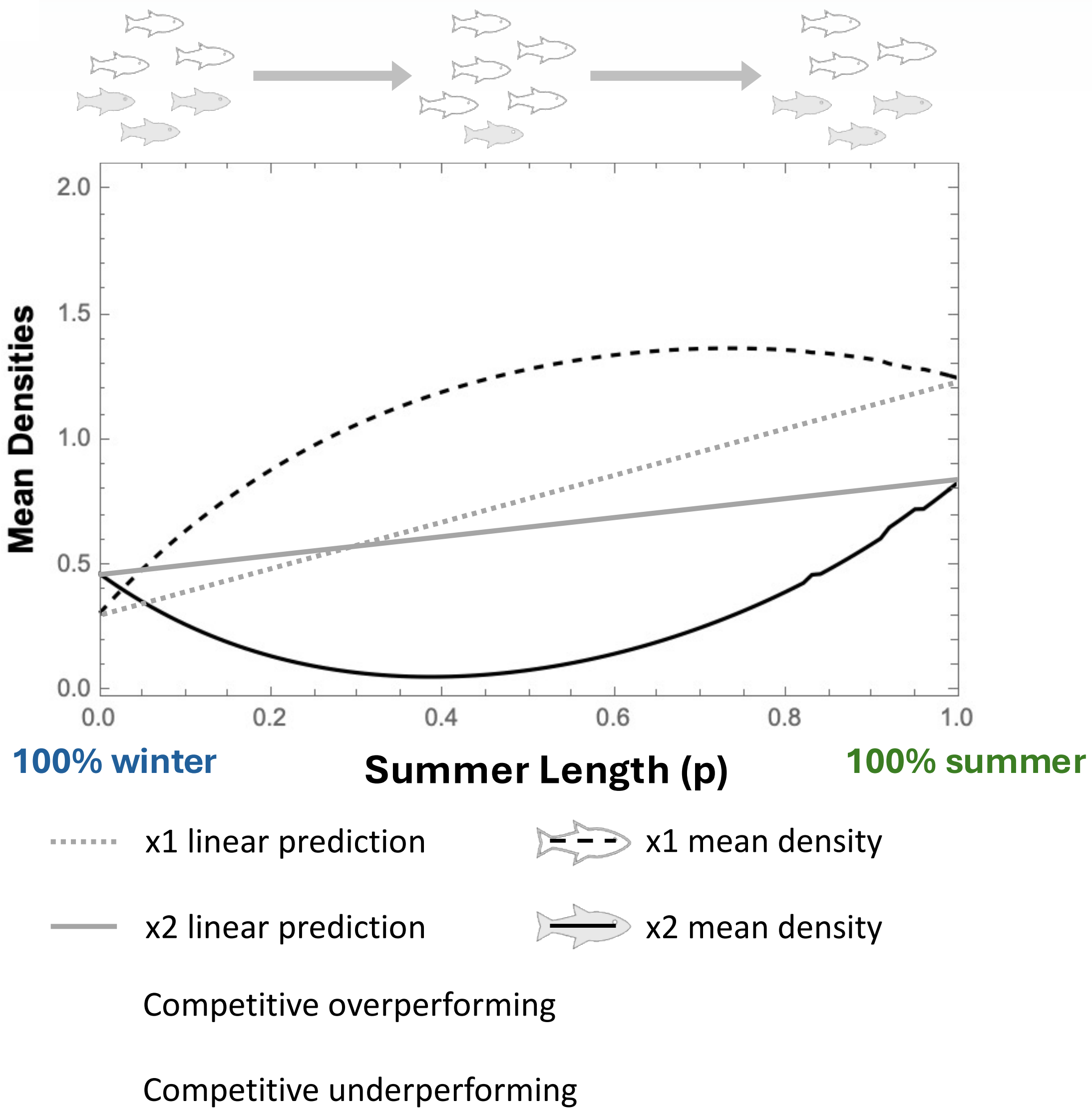
# Intuitive competitive performance



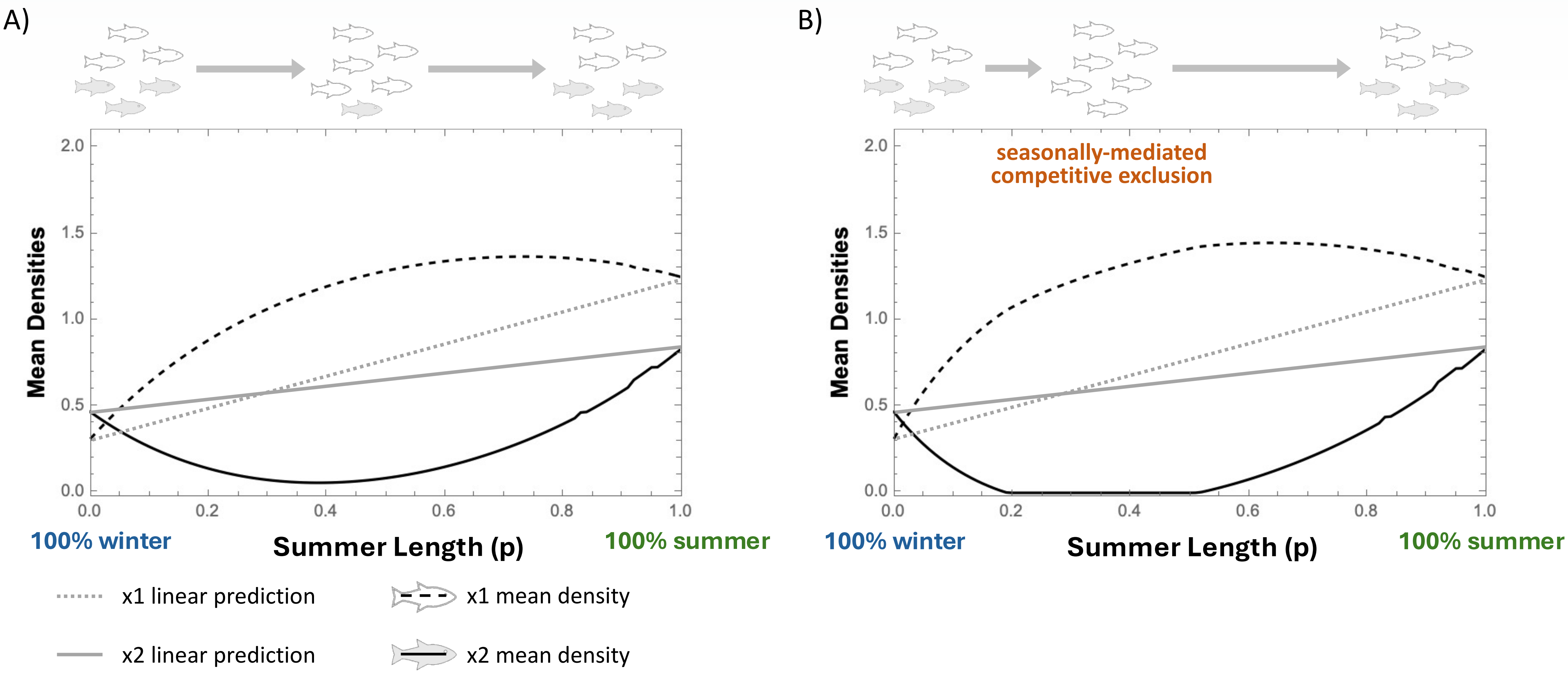

Endpoints @
100% winter & 100% summer
are known from classical **coexistence criteria**
(i.e., no periodicity)

# Counter-intuitive competitive performance




Changing seasonality can have a **nonlinear effect** on species' densities

# Counter-intuitive competitive performance

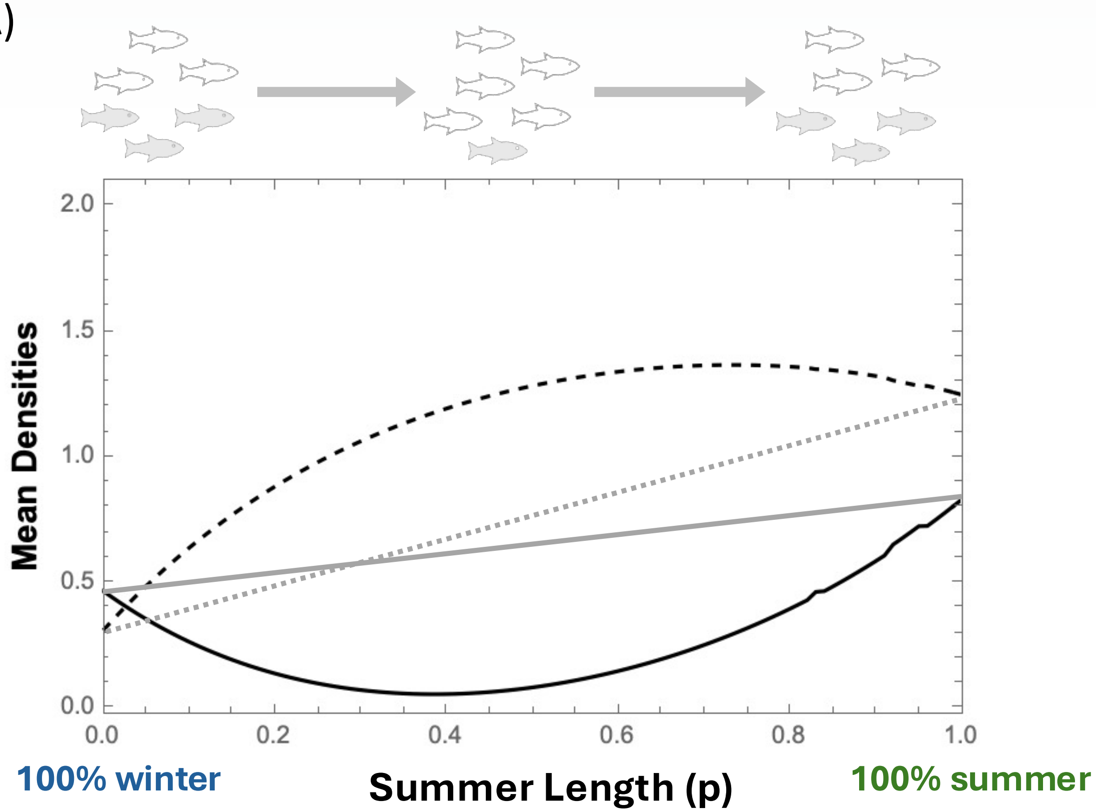



Competitive overperforming

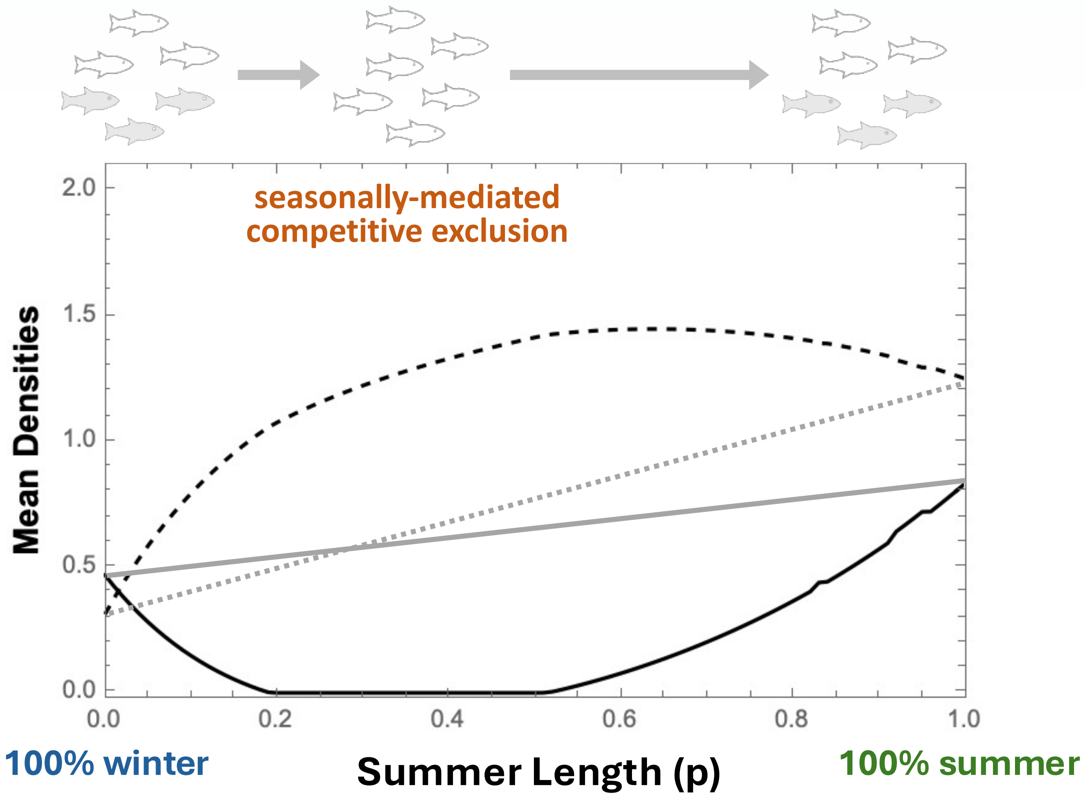
Competitive underperforming

# **Counter**-intuitive competitive performance

A)




B)




x1 linear prediction

x1 mean density

x2 linear prediction

x2 mean density

Competitive overperforming

Competitive underperforming

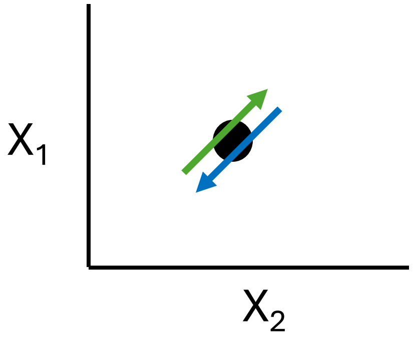
What causes counterintuitive competitive performance?

# Analytical approximation of seasonal coexistence outcomes

$$\frac{dX_{j,s}}{dt} = p\, f_{s,j}(X_j, X_k)$$

$$\frac{dX_{j,w}}{dt} = (1-p) f_{w,j}(X_j, X_k)$$

$$p\, f_{s,j}(X_j, X_k) = -(1-p)\, f_{w,j}(X_j, X_k)$$



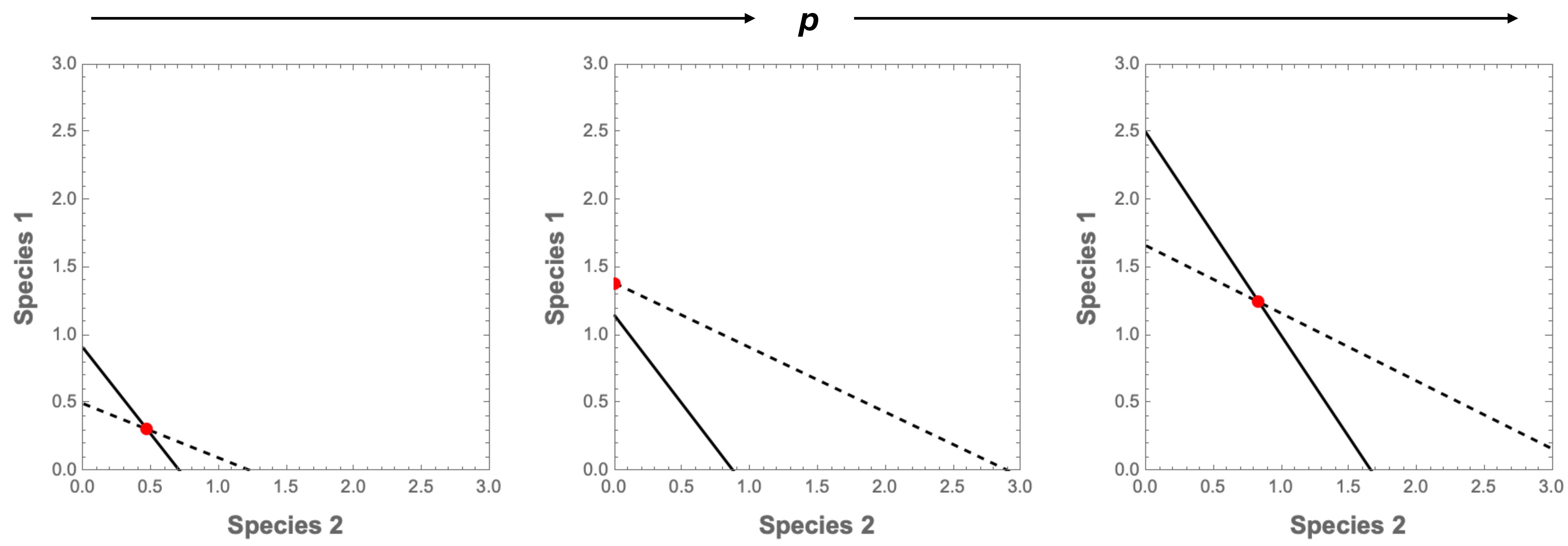

Scott et al. *Biorxiv* DOI:10.1101/2023.02.24.529749

Species 1 approximate isocline:

$$X_1 = \frac{pr_{s,1}(1-\alpha_{s,12}X_2) + (1-p)r_{w,1}(1-\alpha_{w,12}X_2)}{p\alpha_{s,11}r_{s,1} + (1-p)\alpha_{w,11}r_{w,1}}$$

Species 2 approximate isocline:

$$X_1 = \frac{pr_{s,2}(1-\alpha_{s,22}X_2) + (1-p)r_{w,2}(1-\alpha_{w,22}X_2)}{p\alpha_{s,21}r_{s,2} + (1-p)\alpha_{w,21}r_{w,2}}$$

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# Seasonal coexistence criteria from approximation

| | | | |
|---|---|---|---|
| Coexistence | $\dfrac{pr_{s,1} + r_{w,1} - pr_{w,1}}{pr_{s,1}\alpha_{s,11} + r_{w,1}a_{w,11} - pr_{w,1}a_{w,11}}$ | $<$ | $\dfrac{pr_{s,2} + r_{w,2} - pr_{w,2}}{pr_{s,2}\alpha_{s,21} + r_{w,2}\alpha_{w,21} - pr_{w,2}\alpha_{w,21}}$ |
| | $\dfrac{pr_{s,2} + r_{w,2} - pr_{w,2}}{pr_{s,2}\alpha_{s,22} + r_{w,2}a_{w,22} - pr_{w,2}a_{w,22}}$ | $<$ | $\dfrac{pr_{s,1} + r_{w,1} - pr_{w,1}}{pr_{s,1}\alpha_{s,12} + r_{w,1}\alpha_{w,12} - pr_{w,1}\alpha_{w,12}}$ |
| Competitive Exclusion by Species 1 | $\dfrac{pr_{s,1} + r_{w,1} - pr_{w,1}}{pr_{s,1}\alpha_{s,11} + r_{w,1}a_{w,11} - pr_{w,1}a_{w,11}}$ | $>$ | $\dfrac{pr_{s,2} + r_{w,2} - pr_{w,2}}{pr_{s,2}\alpha_{s,21} + r_{w,2}\alpha_{w,21} - pr_{w,2}\alpha_{w,21}}$ |
| | $\dfrac{pr_{s,2} + r_{w,2} - pr_{w,2}}{pr_{s,2}\alpha_{s,22} + r_{w,2}a_{w,22} - pr_{w,2}a_{w,22}}$ | $<$ | $\dfrac{pr_{s,1} + r_{w,1} - pr_{w,1}}{pr_{s,1}\alpha_{s,12} + r_{w,1}\alpha_{w,12} - pr_{w,1}\alpha_{w,12}}$ |

# Seasonal coexistence criteria from approximation

| | | | |
|---|---|---|---|
| Coexistence | $\frac{pr_{s,1}+r_{w,1}-pr_{w,1}}{pr_{s,1}\alpha_{s,11}+r_{w,1}\alpha_{w,11}-pr_{w,1}\alpha_{w,11}} \sim \frac{1}{\alpha_{11}}$ | $<$ | $\frac{pr_{s,2}+r_{w,2}-pr_{w,2}}{pr_{s,2}\alpha_{s,21}+r_{w,2}\alpha_{w,21}-pr_{w,2}\alpha_{w,21}} \sim \frac{1}{\alpha_{21}}$ |
| | $\frac{pr_{s,2}+r_{w,2}-pr_{w,2}}{pr_{s,2}\alpha_{s,22}+r_{w,2}\alpha_{w,22}-pr_{w,2}\alpha_{w,22}} \sim \frac{1}{\alpha_{22}}$ | $<$ | $\frac{pr_{s,1}+r_{w,1}-pr_{w,1}}{pr_{s,1}\alpha_{s,12}+r_{w,1}\alpha_{w,12}-pr_{w,1}\alpha_{w,12}} \sim \frac{1}{\alpha_{12}}$ |
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| | $\frac{pr_{s,2}+r_{w,2}-pr_{w,2}}{pr_{s,2}\alpha_{s,22}+r_{w,2}\alpha_{w,22}-pr_{w,2}\alpha_{w,22}}$ | $<$ | $\frac{pr_{s,1}+r_{w,1}-pr_{w,1}}{pr_{s,1}\alpha_{s,12}+r_{w,1}\alpha_{w,12}-pr_{w,1}\alpha_{w,12}}$ |

# Drivers of “competitive underperformance” of species 2

| | | | |
|---|---|---|---|
| Coexistence | $\frac{pr_{s,1} + r_{w,1} - pr_{w,1}}{pr_{s,1}\alpha_{s,11} + r_{w,1}\alpha_{w,11} - pr_{w,1}\alpha_{w,11}}$ | **<** | $\frac{pr_{s,2} + r_{w,2} - pr_{w,2}}{pr_{s,2}\alpha_{s,21} + r_{w,2}\alpha_{w,21} - pr_{w,2}\alpha_{w,21}}$ |
| | $\frac{pr_{s,2} + r_{w,2} - pr_{w,2}}{pr_{s,2}\alpha_{s,22} + r_{w,2}\alpha_{w,22} - pr_{w,2}\alpha_{w,22}}$ | **<** | $\frac{pr_{s,1} + r_{w,1} - pr_{w,1}}{pr_{s,1}\alpha_{s,12} + r_{w,1}\alpha_{w,12} - pr_{w,1}\alpha_{w,12}}$ |
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| | $\frac{pr_{s,2}+r_{w,2}-pr_{w,2}}{pr_{s,2}\alpha_{s,22}+r_{w,2}\alpha_{w,22}-pr_{w,2}\alpha_{w,22}}$ | $<$ | $\frac{pr_{s,1}+r_{w,1}-pr_{w,1}}{pr_{s,1}\alpha_{s,12}+r_{w,1}\alpha_{w,12}-pr_{w,1}\alpha_{w,12}}$ |
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| | $\frac{pr_{s,2}+r_{w,2}-pr_{w,2}}{pr_{s,2}\alpha_{s,22}+r_{w,2}\alpha_{w,22}-pr_{w,2}\alpha_{w,22}}$ | $<$ | $\frac{pr_{s,1}+r_{w,1}-pr_{w,1}}{pr_{s,1}\alpha_{s,12}+r_{w,1}\alpha_{w,12}-pr_{w,1}\alpha_{w,12}}$ |

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| | $\frac{pr_{s,2} + r_{w,2} - pr_{w,2}}{pr_{s,2}\alpha_{s,22} + r_{w,2}a_{w,22} - pr_{w,2}a_{w,22}}$ | $<$ | $\frac{pr_{s,1} + r_{w,1} - pr_{w,1}}{pr_{s,1}\alpha_{s,12} + r_{w,1}\alpha_{w,12} - pr_{w,1}\alpha_{w,12}}$ |
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| | $\frac{pr_{s,2} + r_{w,2} - pr_{w,2}}{pr_{s,2}\alpha_{s,22} + r_{w,2}a_{w,22} - pr_{w,2}a_{w,22}}$ | $<$ | $\frac{pr_{s,1} + r_{w,1} - pr_{w,1}}{pr_{s,1}\alpha_{s,12} + r_{w,1}\alpha_{w,12} - pr_{w,1}\alpha_{w,12}}$ |

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| | | | |
|---|---|---|---|
| Coexistence | $\frac{pr_{s,1}+r_{w,1}-pr_{w,1}}{pr_{s,1}\alpha_{s,11}+r_{w,1}\alpha_{w,11}-pr_{w,1}\alpha_{w,11}}$ | $<$ | $\frac{pr_{s,2}+r_{w,2}-pr_{w,2}}{pr_{s,2}\alpha_{s,21}+r_{w,2}\alpha_{w,21}-pr_{w,2}\alpha_{w,21}}$ |
| | $\frac{pr_{s,2}+r_{w,2}-pr_{w,2}}{pr_{s,2}\alpha_{s,22}+r_{w,2}\alpha_{w,22}-pr_{w,2}\alpha_{w,22}}$ | $<$ | $\frac{pr_{s,1}+r_{w,1}-pr_{w,1}}{pr_{s,1}\alpha_{s,12}+r_{w,1}\alpha_{w,12}-pr_{w,1}\alpha_{w,12}}$ |
| Competitive Exclusion by Species 1 | $\frac{pr_{s,1}+r_{w,1}-pr_{w,1}}{pr_{s,1}\alpha_{s,11}+r_{w,1}\alpha_{w,11}-pr_{w,1}\alpha_{w,11}}$ | $>$ | $\frac{pr_{s,2}+r_{w,2}-pr_{w,2}}{pr_{s,2}\alpha_{s,21}+r_{w,2}\alpha_{w,21}-pr_{w,2}\alpha_{w,21}}$ |
| | $\frac{pr_{s,2}+r_{w,2}-pr_{w,2}}{pr_{s,2}\alpha_{s,22}+r_{w,2}\alpha_{w,22}-pr_{w,2}\alpha_{w,22}}$ | $<$ | $\frac{pr_{s,1}+r_{w,1}-pr_{w,1}}{pr_{s,1}\alpha_{s,12}+r_{w,1}\alpha_{w,12}-pr_{w,1}\alpha_{w,12}}$ |

# Drivers of “competitive underperformance” of species 2

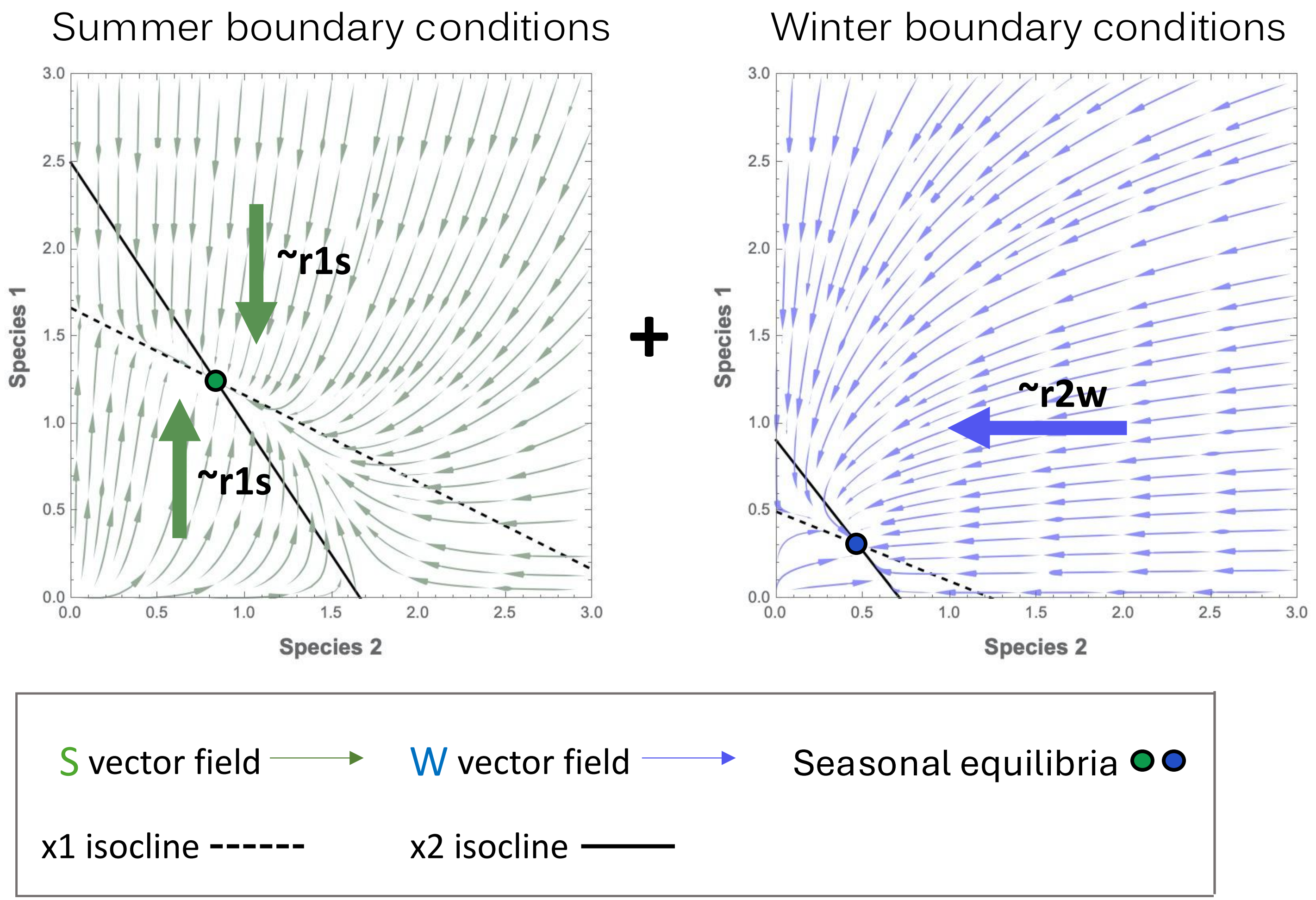
| | | | |
|---|---|---|---|
| Coexistence | $\frac{pr_{s,1} + r_{w,1} - pr_{w,1}}{pr_{s,1}\alpha_{s,11} + r_{w,1}\alpha_{w,11} - pr_{w,1}\alpha_{w,11}}$ | $<$ | $\frac{pr_{s,2} + r_{w,2} - pr_{w,2}}{pr_{s,2}\alpha_{s,21} + r_{w,2}\alpha_{w,21} - pr_{w,2}\alpha_{w,21}}$ |
| | $\frac{pr_{s,2} + r_{w,2} - pr_{w,2}}{pr_{s,2}\alpha_{s,22} + r_{w,2}\alpha_{w,22} - pr_{w,2}\alpha_{w,22}}$ | $<$ | $\frac{pr_{s,1} + r_{w,1} - pr_{w,1}}{pr_{s,1}\alpha_{s,12} + r_{w,1}\alpha_{w,12} - pr_{w,1}\alpha_{w,12}}$ |
| Competitive Exclusion by Species 1 | $\frac{pr_{s,1} + r_{w,1} - pr_{w,1}}{pr_{s,1}\alpha_{s,11} + r_{w,1}\alpha_{w,11} - pr_{w,1}\alpha_{w,11}}$ | $>$ | $\frac{pr_{s,2} + r_{w,2} - pr_{w,2}}{pr_{s,2}\alpha_{s,21} + r_{w,2}\alpha_{w,21} - pr_{w,2}\alpha_{w,21}}$ |
| | $\frac{pr_{s,2} + r_{w,2} - pr_{w,2}}{pr_{s,2}\alpha_{s,22} + r_{w,2}\alpha_{w,22} - pr_{w,2}\alpha_{w,22}}$ | $<$ | $\frac{pr_{s,1} + r_{w,1} - pr_{w,1}}{pr_{s,1}\alpha_{s,12} + r_{w,1}\alpha_{w,12} - pr_{w,1}\alpha_{w,12}}$ |

# Drivers of “competitive underperformance” of species 2

| | | |
|---|---|---|
| 1a | $r_{s,1} > r_{s,2}$ | seasonal growth trade-off effect |
| 1b | $r_{w,1} < r_{w,2}$ | |
| 2 | $\alpha_{w,11} > \alpha_{s,11}$ | seasonal competition effect |
| 3 | $\alpha_{11} \approx \alpha_{21}$ | “sister species” effect * |

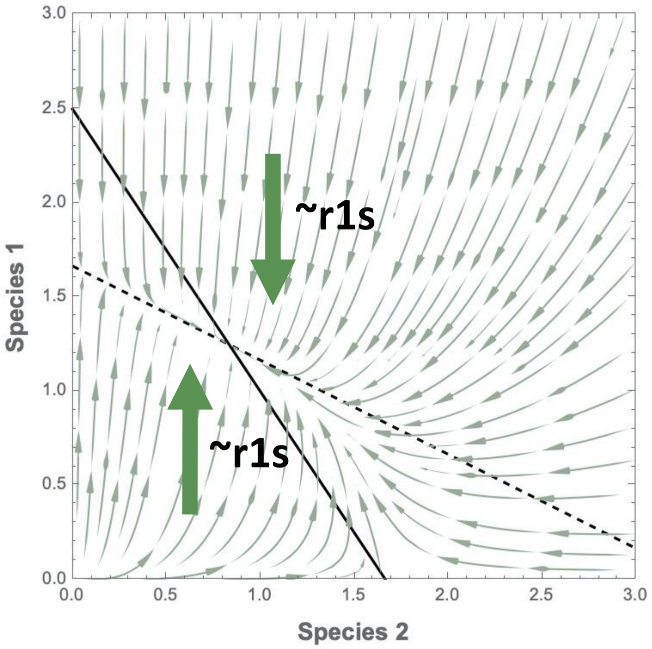
* Amplifies effect, but less prone to driving bifurcation

# Interacting non-local dynamics create a “ratchet effect”



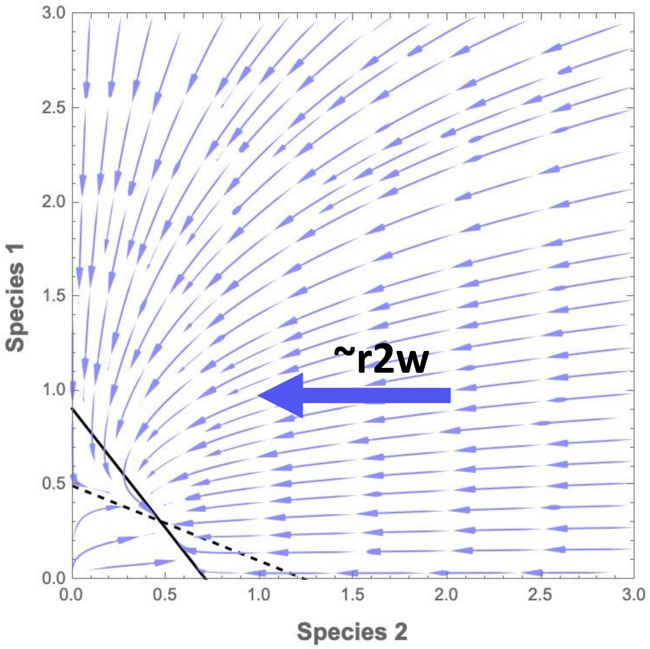
# Interacting non-local dynamics create a "ratchet effect"

Summer boundary conditions




+

Winter boundary conditions

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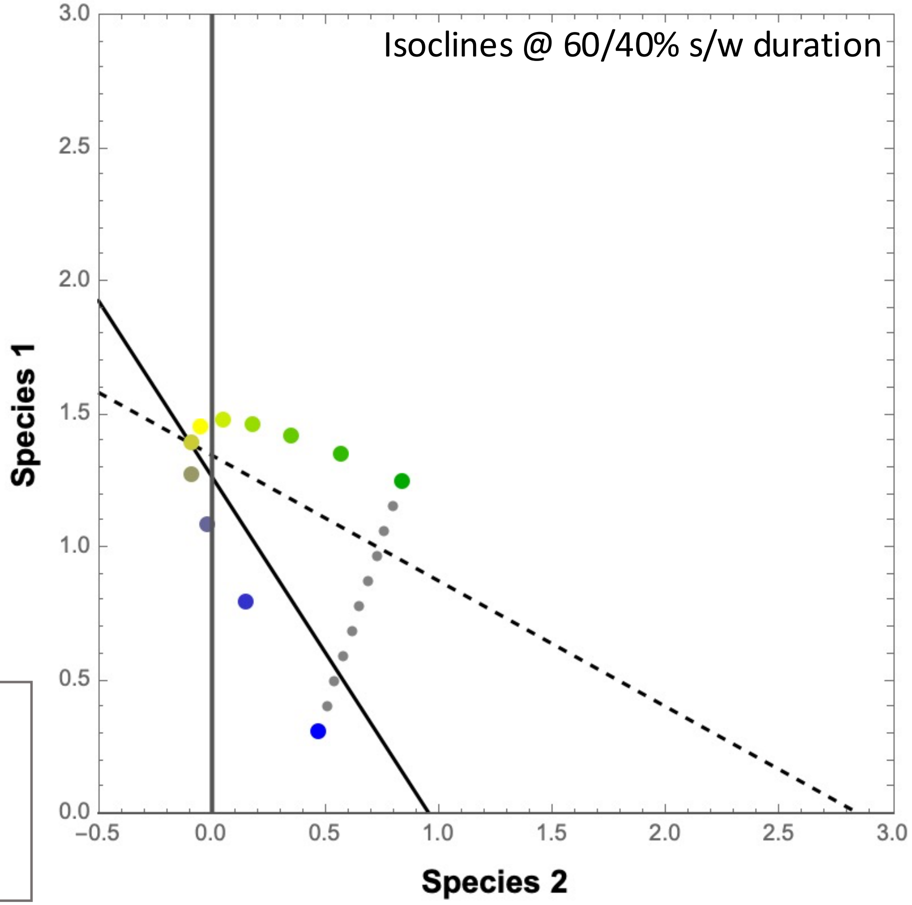
**Overall Effect (approx. isoclines)**



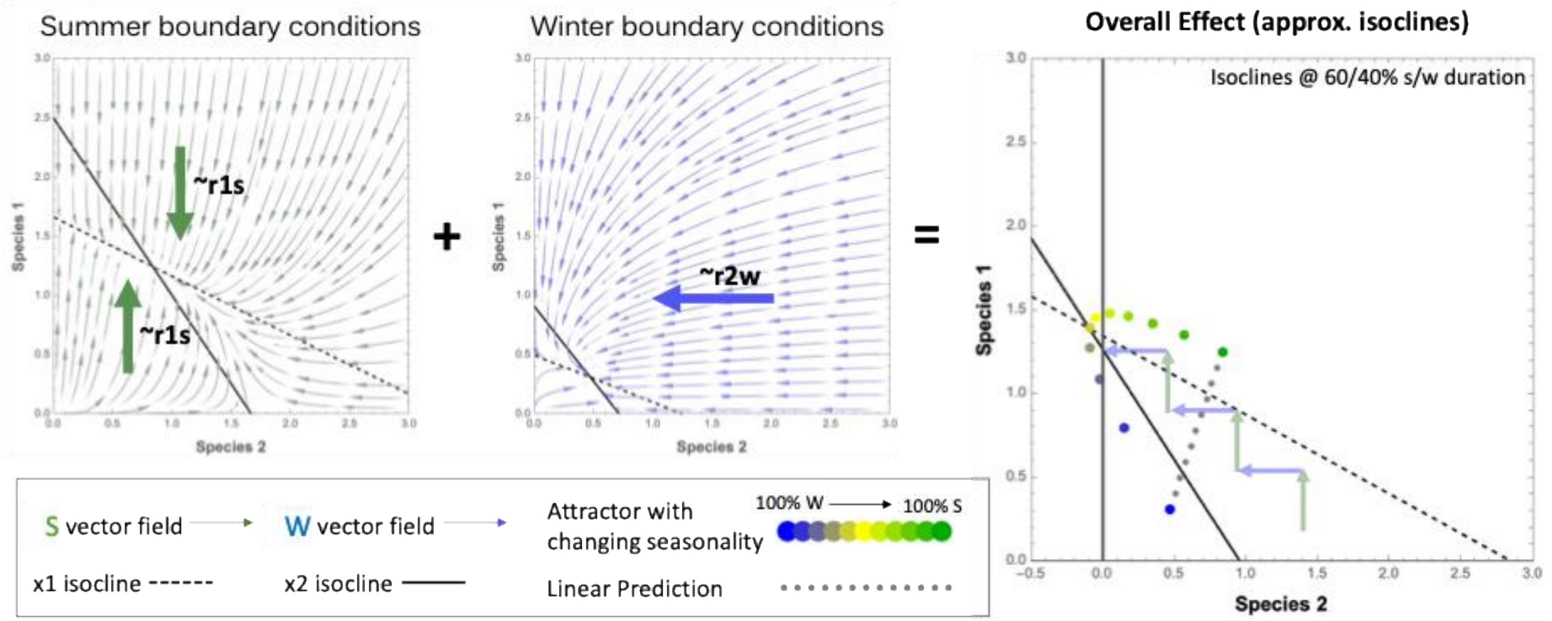

S vector field → W vector field →

x1 isocline ------ x2 isocline ——

Attractor with changing seasonality (100% W → 100% S)

Linear Prediction

# Interacting non-local dynamics create a "ratchet effect"




Counterintuitive competitive performance is driven by:

- Seasonal **growth rate** trade-offs between species (due to differential adaptations to changing conditions) that linearize vector fields
- Seasonal differences in **competition strength** (due to competitive performance or available resources) cause seasonal attractors to diverge
- High **niche overlap** between species (e.g., "sister species") modify non-equilibrium trajectories

# How do fluctuations in the environment affect the structure and function of ecological systems?

In many cases, ecological structure and/or functioning in variable environments is fundamentally different from what deterministic theory would predict.

… & sometimes the outcomes are outside the range of possibilities expected from deterministic theory.

BUT these outcomes are emergent properties of underlying processes, which we can understand.

… for understanding the generality & relevance of outcomes, biological context is important.

Thank you.

# Questions?