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<http://lukaseigentler.github.io>

# Can we predict wavelength changes of patterned ecosystems?

Mathematical modeling of complex biological systems

22 September 2025

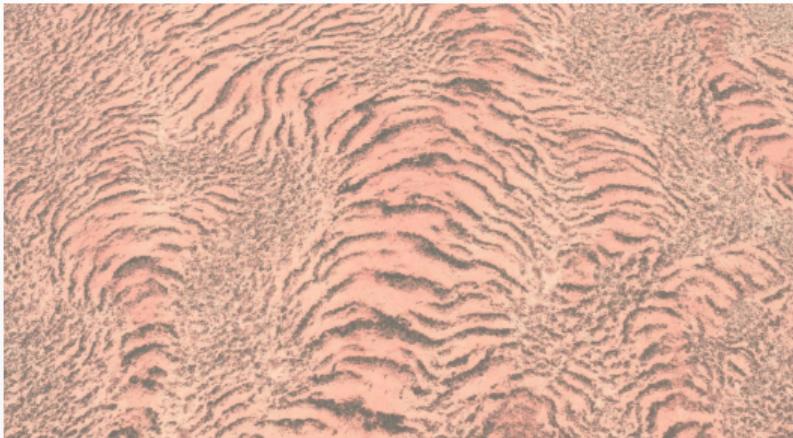
*Lukas Eigentler (University of Warwick, UK)*

*joint work with Mattia Sensi (University of Trento, Italy)*

# Stripe patterns

Banded vegetation patterns and intertidal mussel beds are classic examples of **self-organisation principles** in ecology.

Vegetation stripes in Ethiopia.



Intertidal mussel beds in the Wadden Sea.



- Parallel to topographic contours and shoreline.
- Caused by a **scale-dependent feedback loop** comprising long-range competition for a limiting resource and short-range facilitation.

# Klausmeier model for vegetation patterns

One of the most basic phenomenological models for vegetation patterns is the **extended Klausmeier reaction-advection-diffusion model**.<sup>1</sup>

$$\begin{aligned}\frac{\partial u}{\partial t} &= \underbrace{u^2 w}_{\text{plant growth}} - \underbrace{Bu}_{\text{plant loss}} + \underbrace{\frac{\partial^2 u}{\partial x^2}}_{\text{plant dispersal}}, \\ \frac{\partial w}{\partial t} &= \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{u^2 w}_{\text{water uptake by plants}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\text{water flow downhill}} + \underbrace{d \frac{\partial^2 w}{\partial x^2}}_{\text{water diffusion}}.\end{aligned}$$

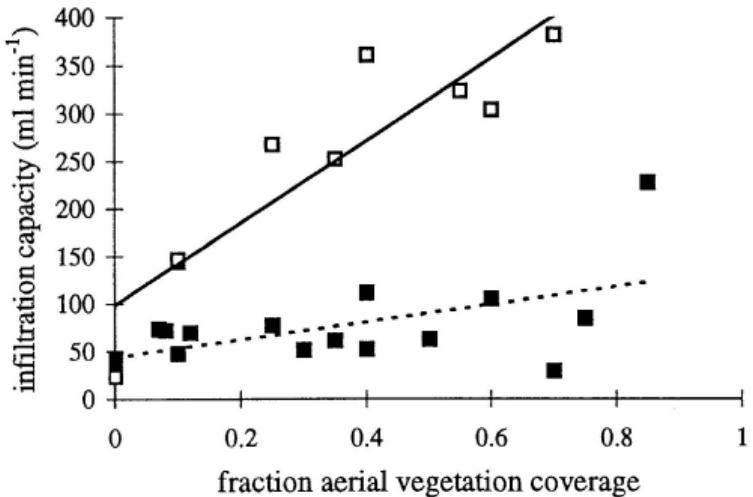
<sup>1</sup> Klausmeier, C. A.: *Science* 284.5421 (1999).

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# Water uptake



Infiltration capacity increases with plant density<sup>2</sup>

The nonlinearity in the water uptake and plant growth terms arises because plants increase the soil's water infiltration capacity.

⇒ Water uptake = Water density × plant density × infiltration rate.

<sup>2</sup>Rietkerk, M. et al.: *Plant Ecol.* 148.2 (2000)

# Klausmeier model for vegetation patterns

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<sup>3</sup>Klausmeier, C. A.: *Science* 284.5421 (1999).

# Sediment accumulation model for mussel beds

A very similar model, the sediment accumulation model describes pattern formation in intertidal mussel beds<sup>4</sup>

$$\begin{aligned}\frac{\partial m}{\partial t} &= \underbrace{\frac{\delta am(s + \eta)}{s + 1}}_{\text{mussel growth}} - \underbrace{\frac{m}{s + 1}}_{\text{mussel death}} + \underbrace{\frac{\partial^2 m}{\partial x^2}}_{\text{mussel dispersal}}, \\ \frac{\partial s}{\partial t} &= \underbrace{\frac{m}{s + 1}}_{\text{sediment build-up}} - \underbrace{\frac{\theta s}{s + 1}}_{\text{sediment erosion}} + \underbrace{\frac{D \frac{\partial^2 s}{\partial x^2}}{s + 1}}_{\text{sediment dispersal}}, \\ \frac{\partial a}{\partial t} &= \underbrace{\frac{1 - \varepsilon a}{s + 1}}_{\text{transport from upper water layers}} - \underbrace{\frac{\beta am(s + \eta)}{s + 1}}_{\text{algae consumption}} + \underbrace{\nu \frac{\partial a}{\partial x}}_{\text{algae flow with tide}}.\end{aligned}$$

<sup>4</sup>Liu, Q.-X. et al.: *Proc. R. Soc. Lond. B.* 279.1739 (2012).

# Periodic travelling waves

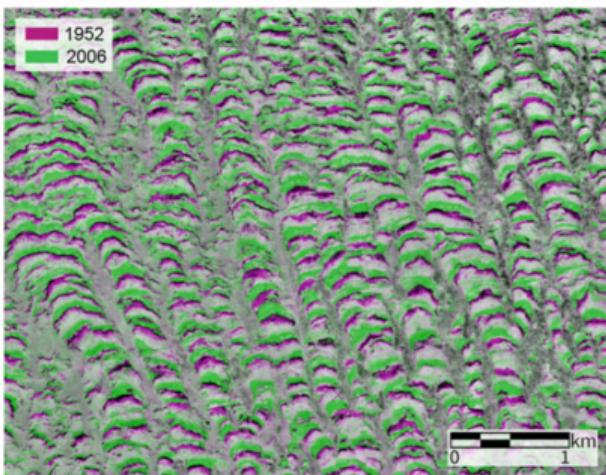
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alternative video link.

- Model represents vegetation patterns as **periodic travelling waves (PTWs)**.

# Uphill movement in ecology

Timeseries data.<sup>5</sup>



Uphill migration due to water gradient.<sup>6</sup>



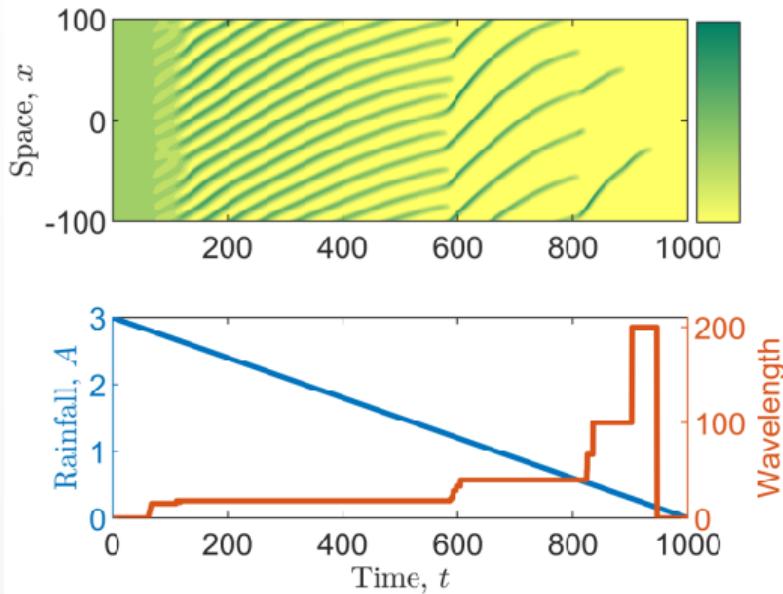
- Data shows that vegetation stripes can move uphill (< 1m per year).

<sup>5</sup> Gandhi, P. et al.: *Dryland ecohydrology*. Springer International Publishing, 2019, pp. 469–509.

<sup>6</sup> Dunkerley, D.: *Desert* 23.2 (2018).

# Periodic travelling waves

alternative video link.



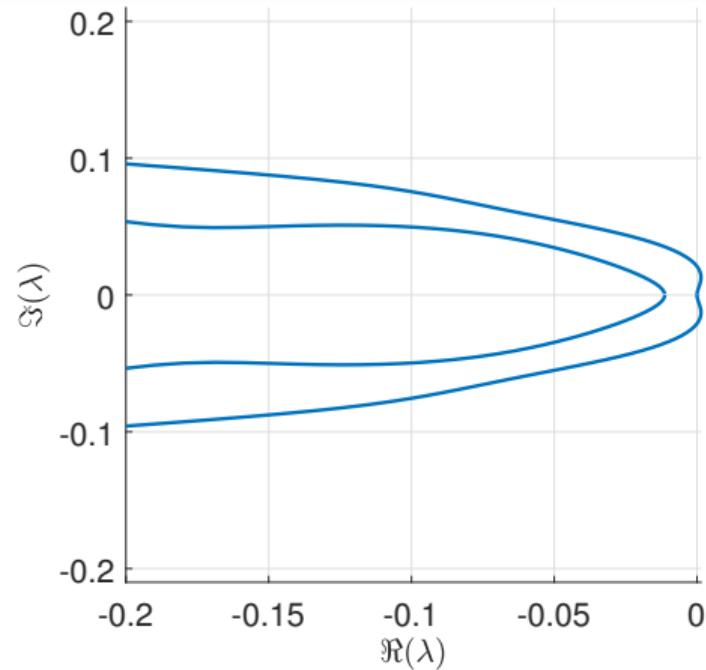
- Model represents vegetation patterns as **periodic travelling waves (PTWs)**.
- Along rainfall gradient, transition from uniform vegetation to desert occurs via several pattern transitions.

# Wavelength changes

- State-of-the-art: predict wavelength changes through PTW stability properties.
- PTW linear stability is determined by their **essential spectra**.
- Calculated using numerical continuation.<sup>a</sup>

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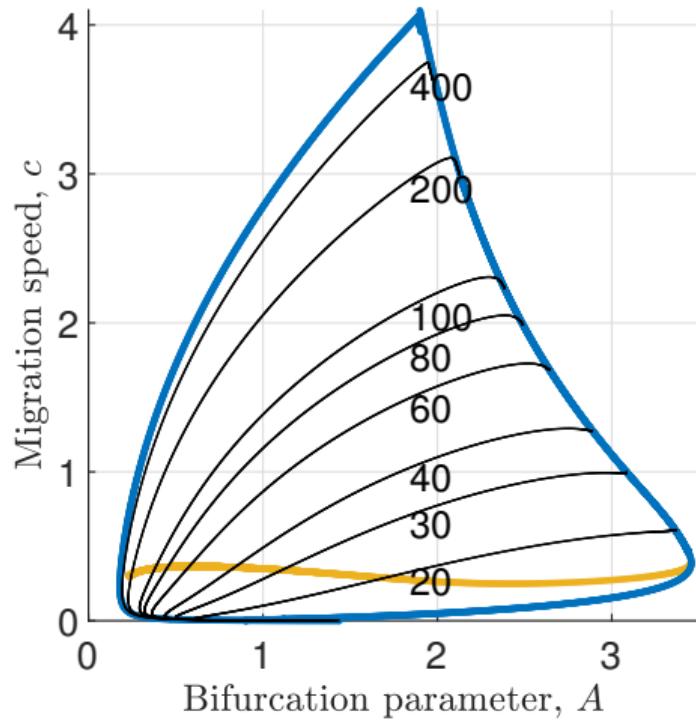
<sup>a</sup>Rademacher, J. D., Sandstede, B. and Scheel, A.: *Physica D* 229.2 (2007).



# Wavelength changes

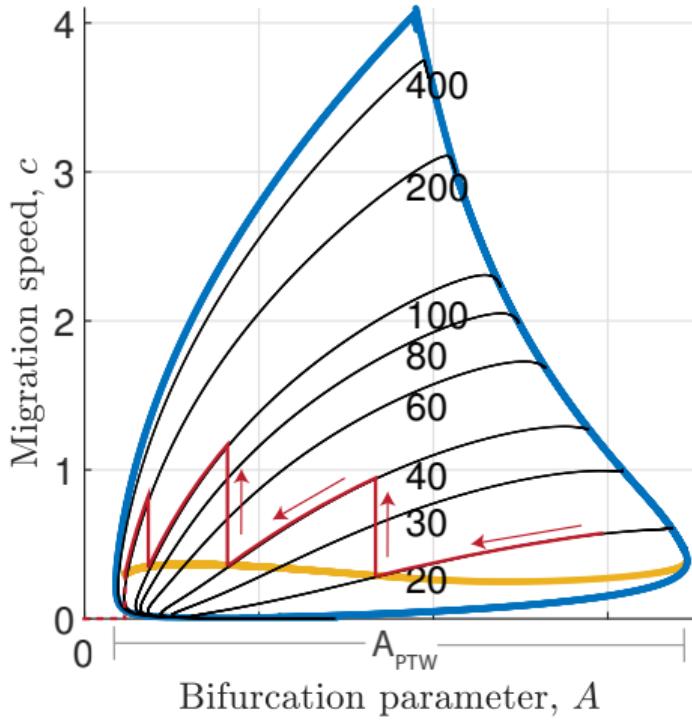
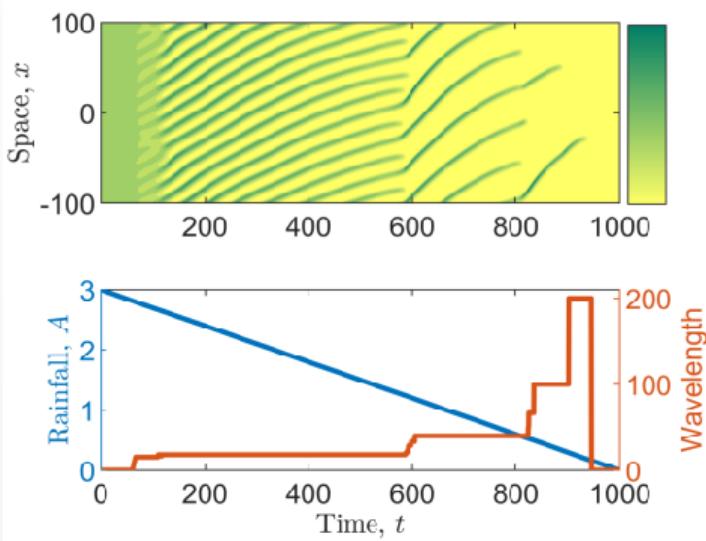
- State-of-the-art: predict wavelength changes through PTW stability properties.
- PTW linear stability is determined by their **essential spectra**.
- Calculated using numerical continuation.<sup>a</sup>
- Wavelengths changes are typically predicted through the *Busse balloon*: parameter space of stable PTWs.

<sup>a</sup>Rademacher, J. D., Sandstede, B. and Scheel, A.: *Physica D* 229.2 (2007).



# Wavelength changes

- Wavelengths are preserved, provided they remain stable.
- Upon destabilisation a wavelength change occurs.



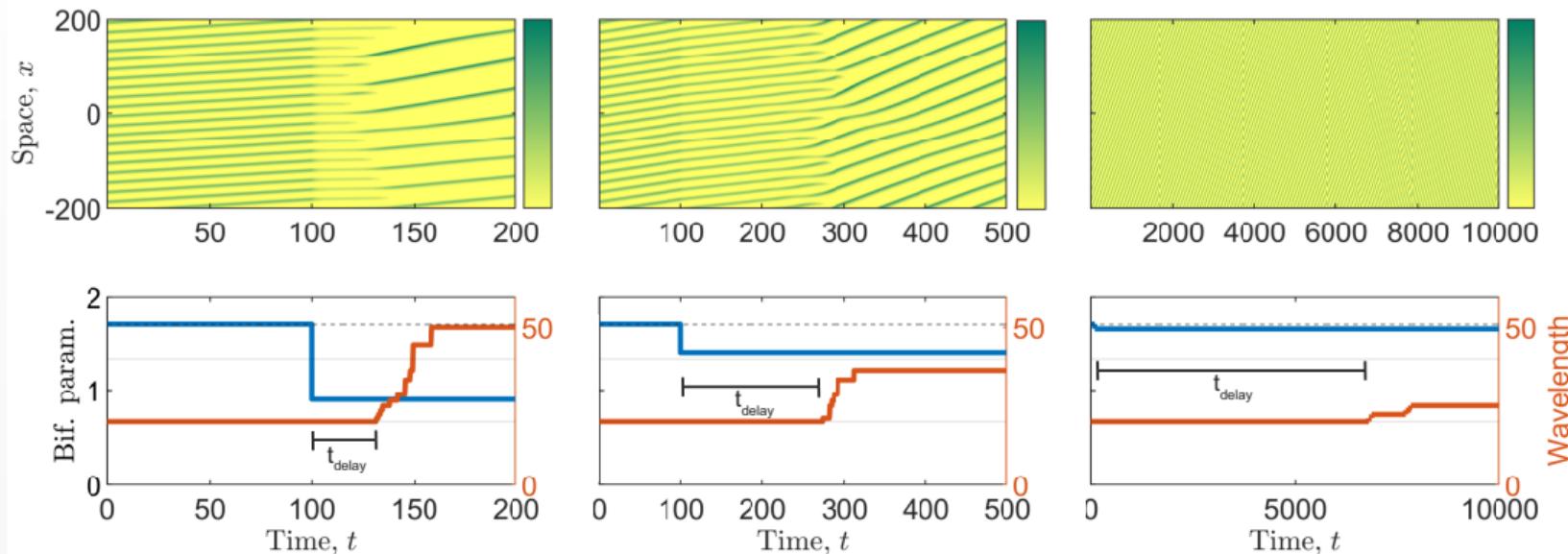
# Wavelength changes

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alternative video link.

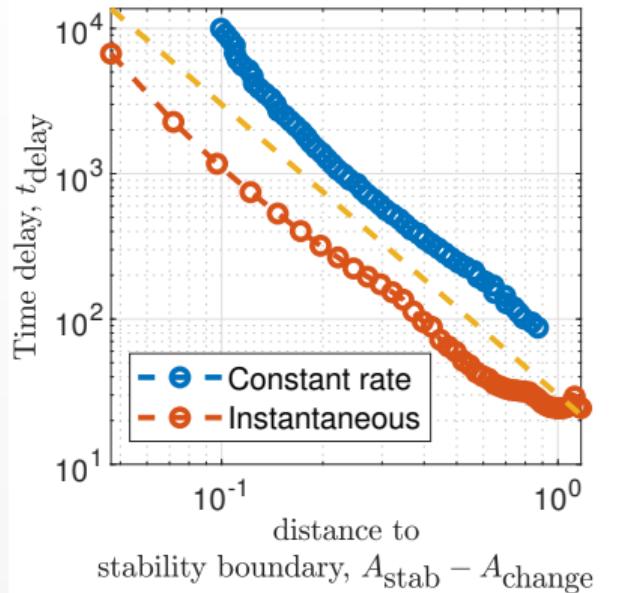
- Significant delays between crossing a stability boundary and observing wavelength changes occur.

# Delays to wavelength changes



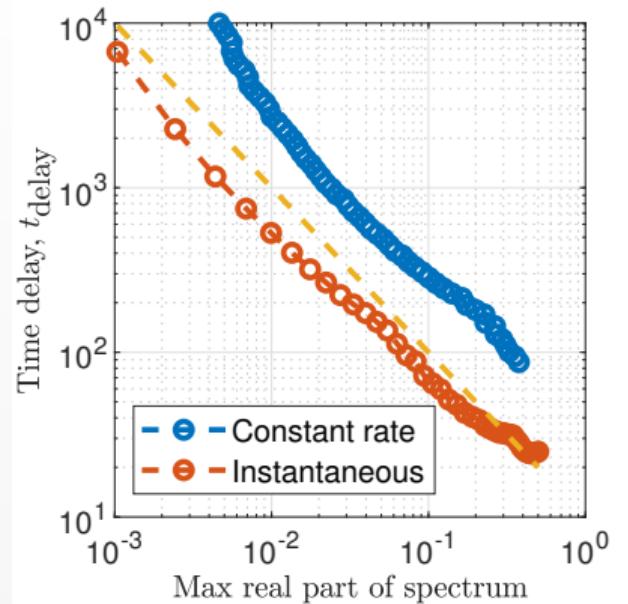
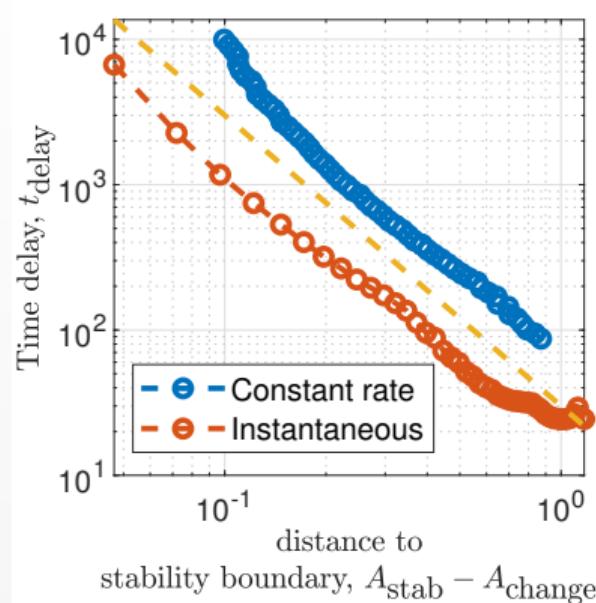
- Significant delays between crossing a stability boundary and observing wavelength changes occur.
- Order of magnitude differences in delay depending on parameter values.

# Predicting delays



There are clear trends between delay and bifurcation parameter

# Predicting delays



There are clear trends between delay and bifurcation parameter and delay and max real part of the spectrum. **no predictive power**

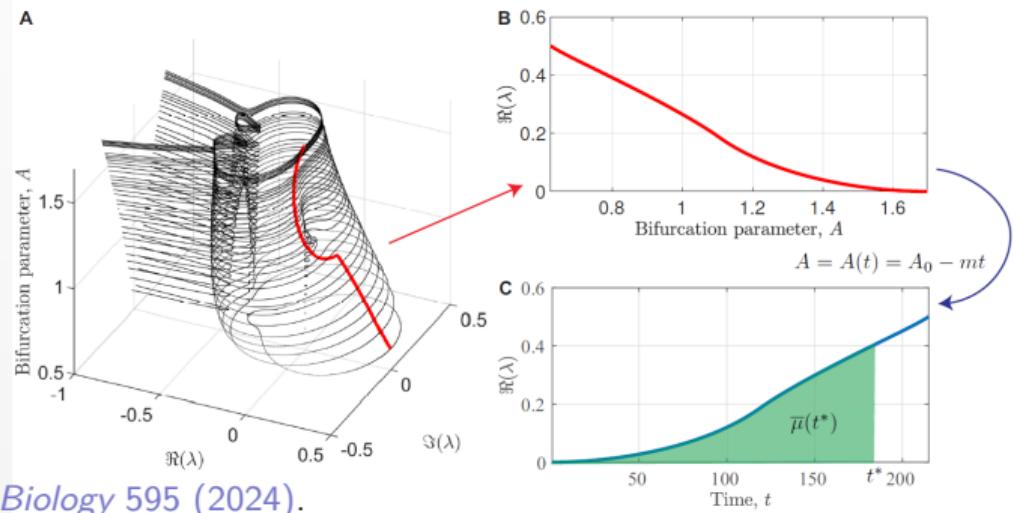
# Predicting delays

Can predict the **order of magnitude of the delay** through the **accumulated maximal instability**<sup>7</sup>

$$\bar{\mu}(A(t)) = \int_{t_{\text{stab}}}^t \mu(\tau) d\tau, \quad t \geq t_{\text{stab}}.$$

$t_{\text{stab}}$  is the time of the last crossing of the stability boundary.

$\mu(t)$  is the max real part of the spectrum at time  $t$ .



<sup>7</sup>EL and Sensi, M.: *Journal of Theoretical Biology* 595 (2024).

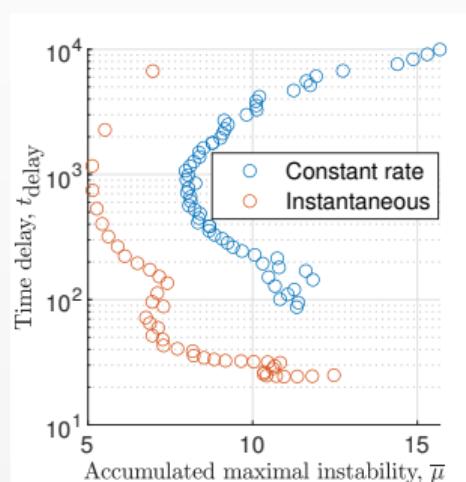
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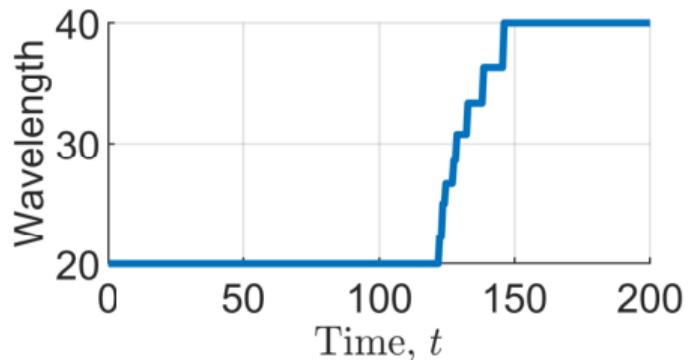
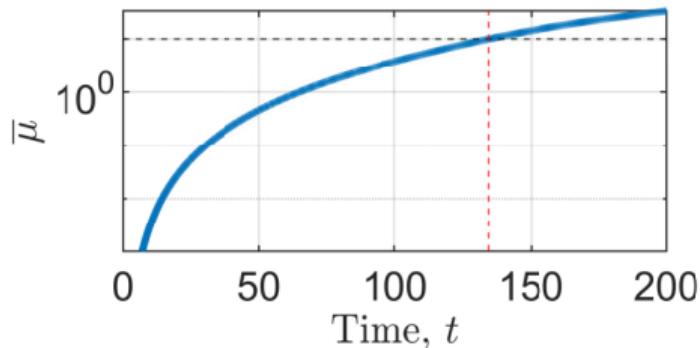
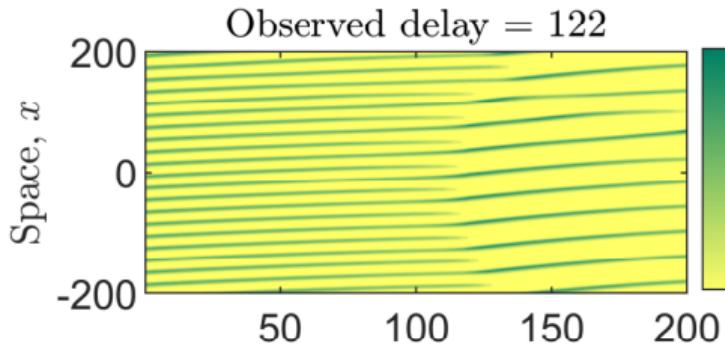
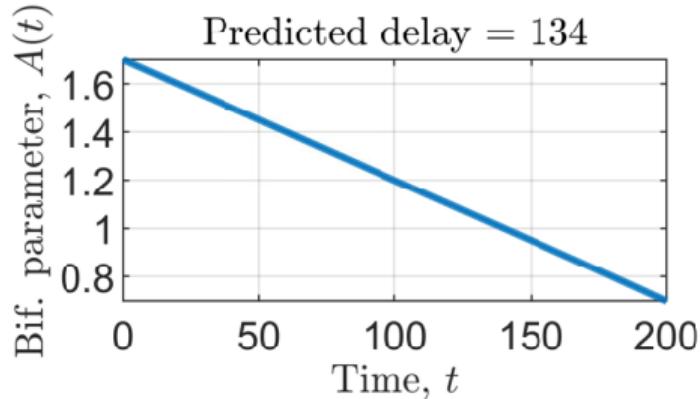
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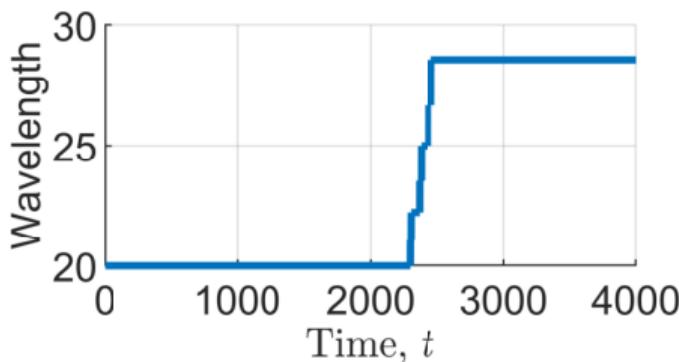
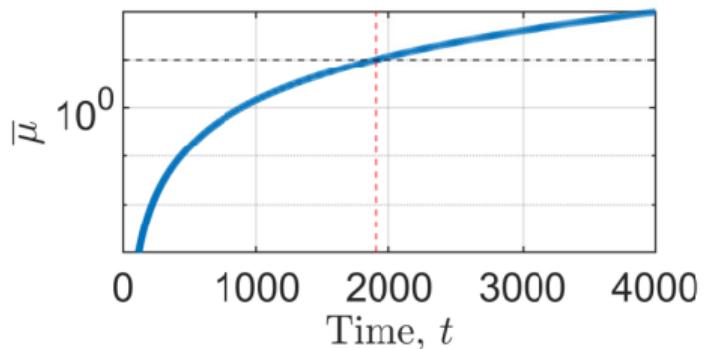
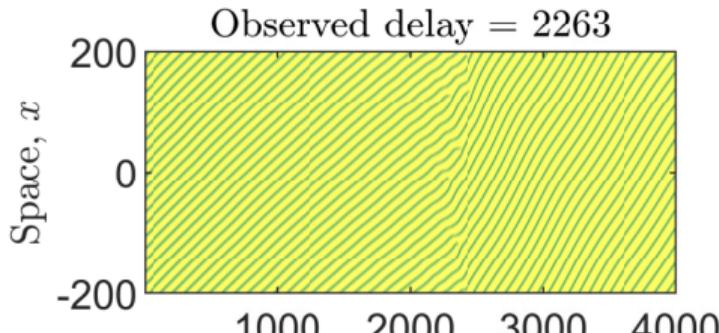
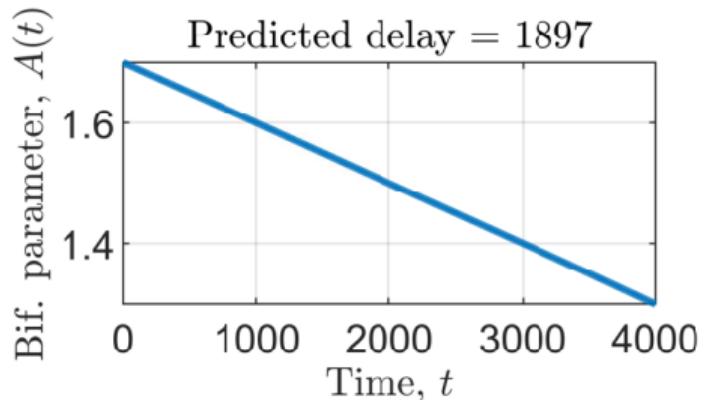
Wavelength change occurs when  $\bar{\mu} \approx 10$

<sup>7</sup>EL and Sensi, M.: *Journal of Theoretical Biology* 595 (2024).

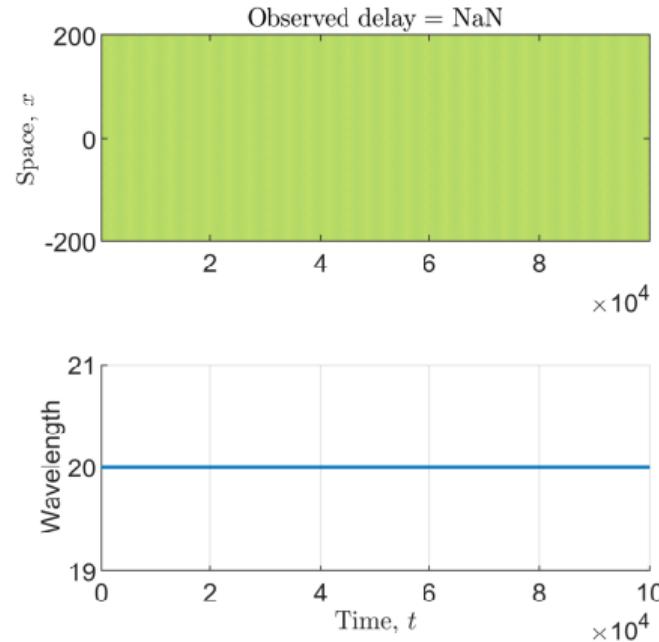
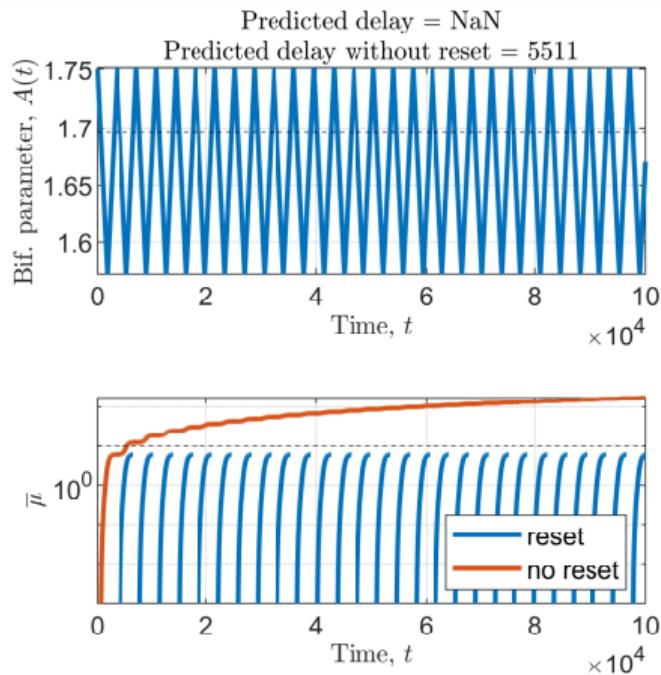
# Delay prediction in practice



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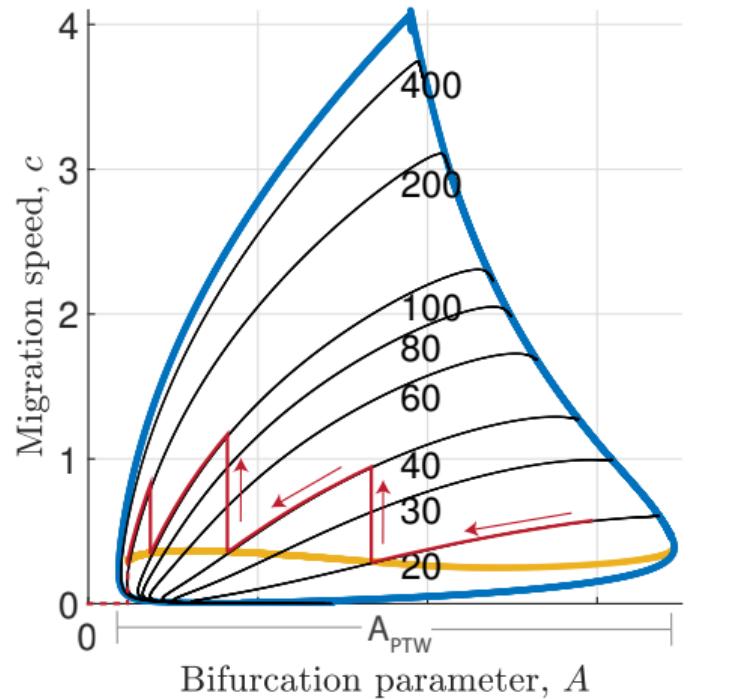


# Delay prediction reset in stable regions



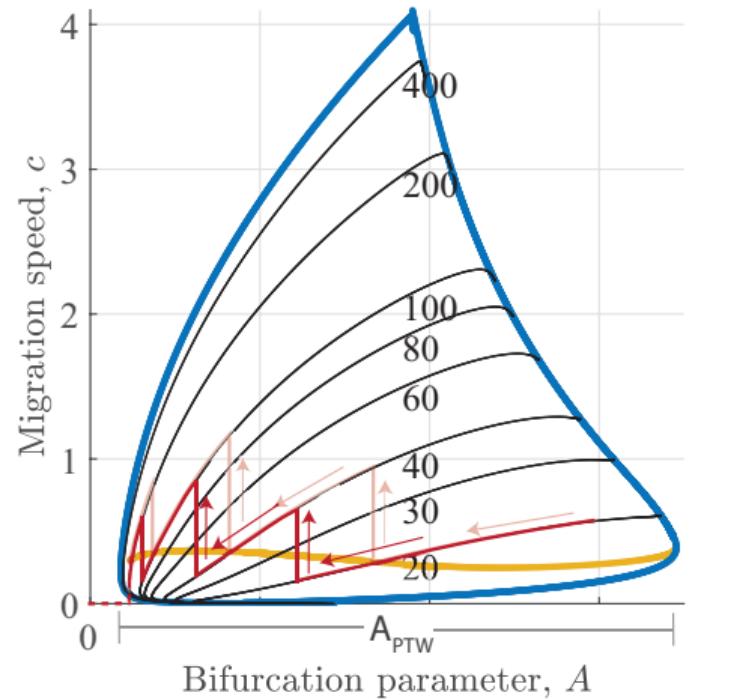
# Conclusions

- Wavelength changes that occur after crossing a stability boundary are subject to a delay.



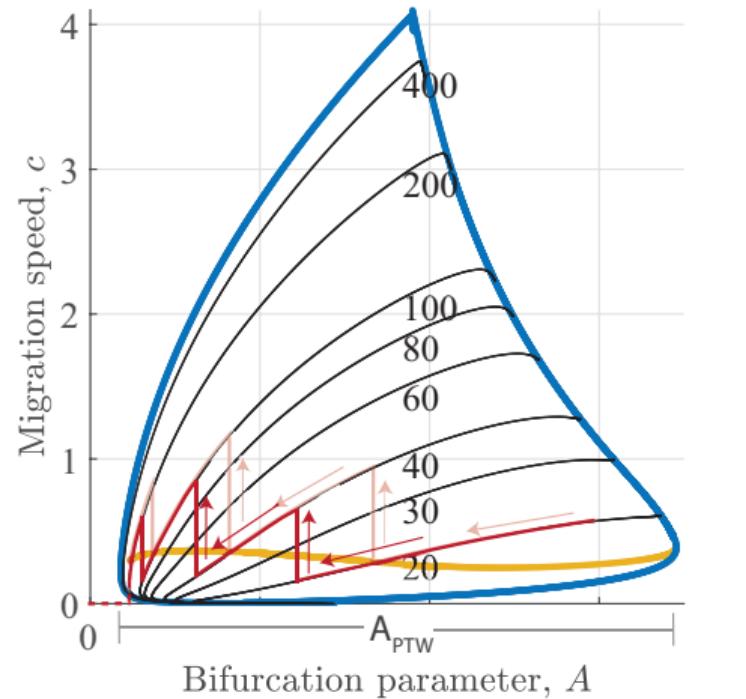
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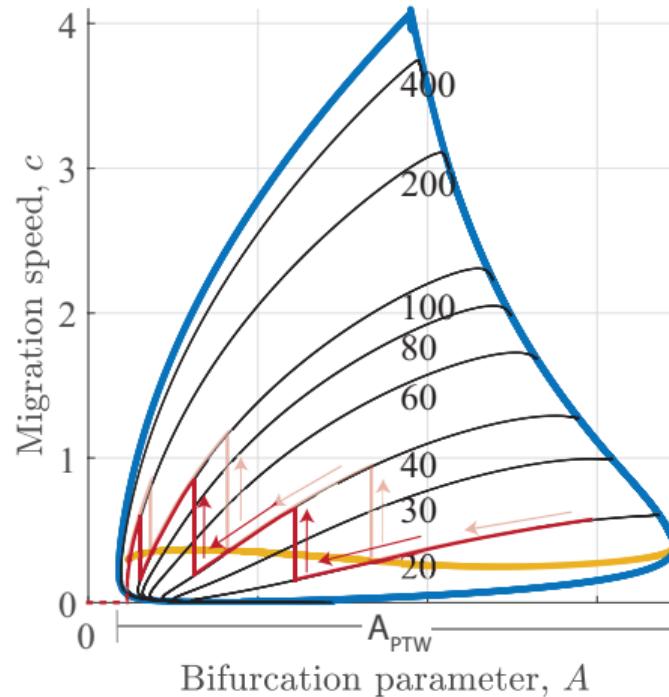
# Conclusions

- Wavelength changes that occur after crossing a stability boundary are subject to a delay.
- Order of magnitude of the delay can be predicted by tracking the maximum real part of the spectrum of the destabilised pattern over time.



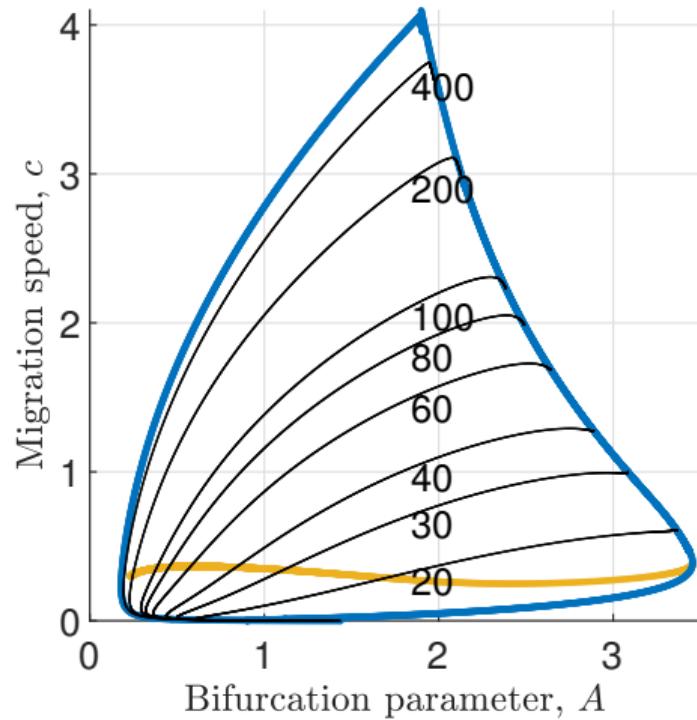
# Conclusions

- Wavelength changes that occur after crossing a stability boundary are subject to a delay.
- Order of magnitude of the delay can be predicted by tracking the maximum real part of the spectrum of the destabilised pattern over time.
- Open question: What new wavelength is chosen?



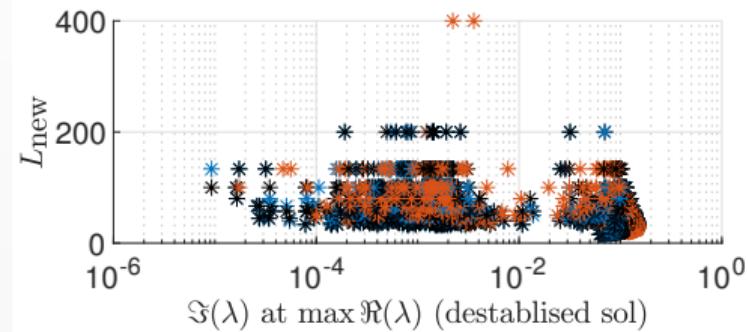
# Wavelength changes

- Open question: What new wavelength is chosen?
- For fixed PDE parameters, there is multistability of different periodic travelling waves.



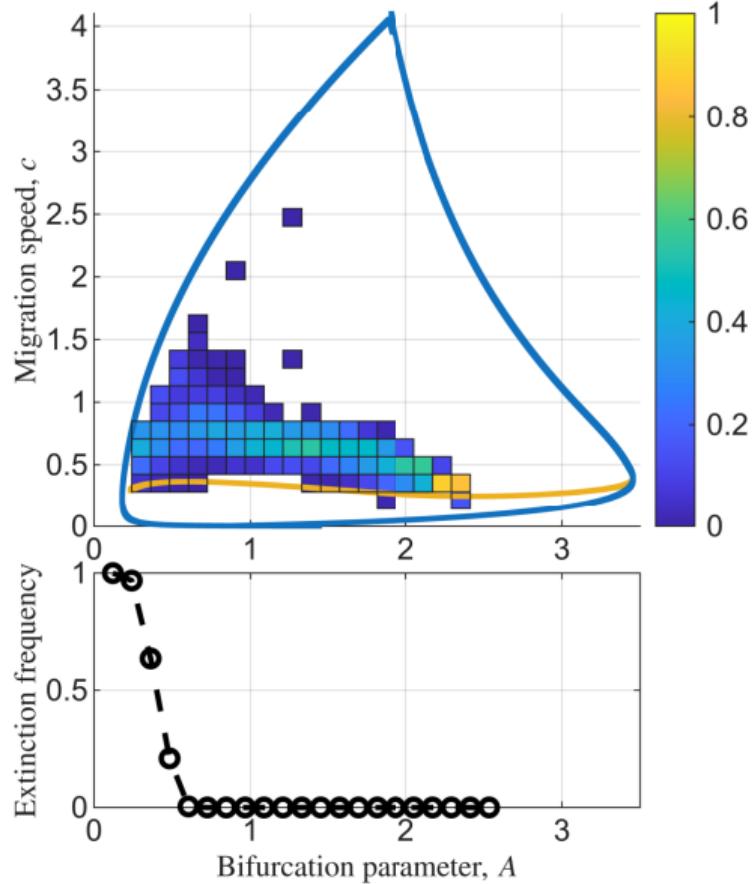
# Linear analysis insufficient

- Created a large dataset of wavelength changes through simulations.
- Compared wavelength change dynamics with features of essential spectra.
- Suggests that **linear analysis is insufficient to characterise wavelength changes.**



## Some selection data

- Large areas of Busse balloon remain unselected.
- Extinction does not necessarily occur at the edge of the Busse balloon.



# What next?

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- New methods needed to understand periodic travelling wave wavelength selection.
- Take inspiration from known results on  $\lambda$ - $\omega$  systems?
- Similar trends observed for mussel model  $\Rightarrow$  possible to derive principles applicable to a wider class of models?
- Need evidence of wavelength changes in empirical systems.

# References

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- [1] Eigentler, L. and Sensi, M.: 'Delayed loss of stability of periodic travelling waves: insights from the analysis of essential spectra'. *Journal of Theoretical Biology* 595 (2024), p. 111945.