Slides are available on my website.
http://lukaseigentler.github.io

Delayed loss of stability of periodic travelling waves affects wavelength changes of patterned ecosystems

M2BE 2025

10 July 2025

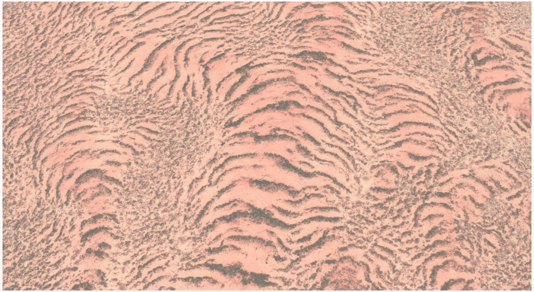
Lukas Eigentler (University of Warwick, UK)

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.

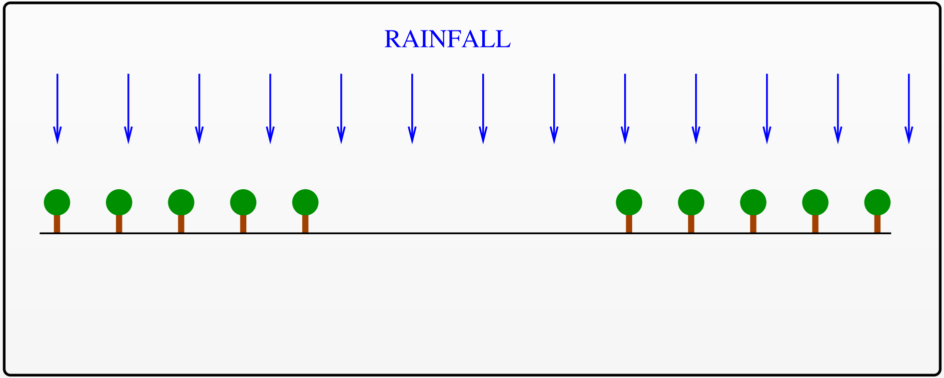


Intertidal mussel beds in the Wadden Sea.

- 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.

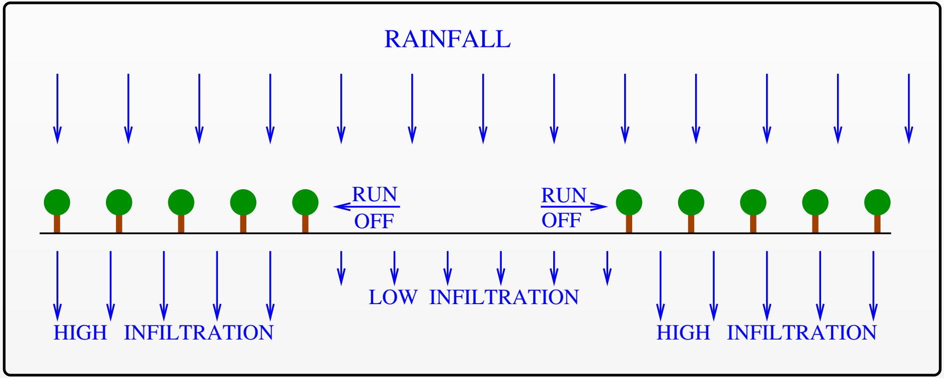
Local facilitation in vegetation patterns

Positive feedback loop: Water infiltration into the soil depends on local plant density $\Rightarrow$ redistribution of water towards existing plant patches $\Rightarrow$ further plant growth.



Local facilitation in vegetation patterns

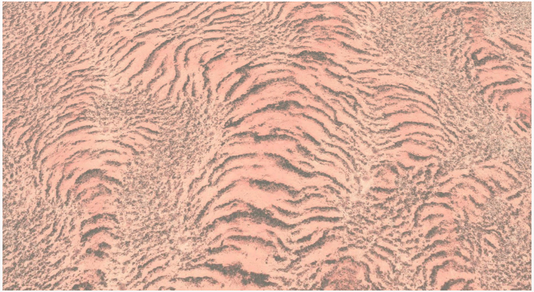
Positive feedback loop: Water infiltration into the soil depends on local plant density ⇒ redistribution of water towards existing plant patches ⇒ further plant growth.



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.[1]

$$\frac{\partial u}{\partial t} = \overbrace{u^2 w}^{\text{plant growth}} - \overbrace{Bu}^{\text{plant loss}} + \overbrace{\frac{\partial^2 u}{\partial x^2}}^{\text{plant dispersal}},$$

$$\frac{\partial w}{\partial t} = \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{u^2 w}_{\substack{\text{water uptake}\\ \text{by plants}}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\substack{\text{water flow}\\ \text{downhill}}} + \underbrace{d \frac{\partial^2 w}{\partial x^2}}_{\substack{\text{water}\\ \text{diffusion}}}.$$

[1] Klausmeier, C. A.: *Science* 284.5421 (1999).

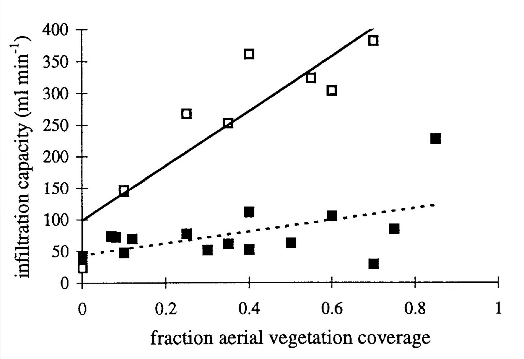
Klausmeier model for vegetation patterns

One of the most basic phenomenological models for vegetation patterns is the extended Klausmeier reaction-advection-diffusion model.

$$\frac{\partial u}{\partial t} = \overbrace{u^2 w}^{\text{plant growth}} - \overbrace{Bu}^{\text{plant loss}} + \overbrace{\frac{\partial^2 u}{\partial x^2}}^{\text{plant dispersal}},$$

$$\frac{\partial w}{\partial t} = \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{u^2 w}_{\substack{\text{water uptake}\\ \text{by plants}}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\substack{\text{water flow}\\ \text{downhill}}} + \underbrace{d \frac{\partial^2 w}{\partial x^2}}_{\substack{\text{water}\\ \text{diffusion}}}.$$

Water uptake



Infiltration capacity increases with plant density[2]

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

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

[2] Rietkerk, M. et al.: *Plant Ecol.* 148.2 (2000)

Klausmeier model for vegetation patterns

One of the most basic phenomenological models is the extended Klausmeier reaction-advection-diffusion model.[3]

$$\frac{\partial u}{\partial t} = \overbrace{u^2 w}^{\text{plant growth}} - \overbrace{Bu}^{\text{plant loss}} + \overbrace{\frac{\partial^2 u}{\partial x^2}}^{\text{plant dispersal}},$$

$$\frac{\partial w}{\partial t} = \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{u^2 w}_{\substack{\text{water uptake}\\ \text{by plants}}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\substack{\text{water flow}\\ \text{downhill}}} + \underbrace{d \frac{\partial^2 w}{\partial x^2}}_{\substack{\text{water}\\ \text{diffusion}}}.$$

[3] 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[4]

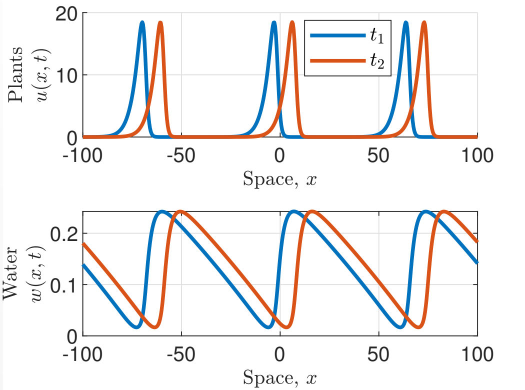
$$\frac{\partial m}{\partial t} = \overbrace{\frac{\delta a m (s+\eta)}{s+1}}^{\text{mussel growth}} - \overbrace{m}^{\text{mussel death}} + \overbrace{\frac{\partial^2 m}{\partial x^2}}^{\text{mussel dispersal}},$$

$$\frac{\partial s}{\partial t} = \underbrace{m}_{\text{sediment build-up}} - \underbrace{\theta s}_{\text{sediment erosion}} + \underbrace{D\frac{\partial^2 s}{\partial x^2}}_{\text{sediment dispersal}},$$

$$\frac{\partial a}{\partial t} = \underbrace{1-\varepsilon a}_{\substack{\text{transport from}\\ \text{upper water layers}}} - \underbrace{\frac{\beta a m (s+\eta)}{s+1}}_{\text{algae consumption}} + \underbrace{\nu \frac{\partial a}{\partial x}}_{\substack{\text{algae flow}\\ \text{with tide}}}.$$

[4] Liu, Q.-X. et al.: *Proc. R. Soc. Lond. B.* 279.1739 (2012).

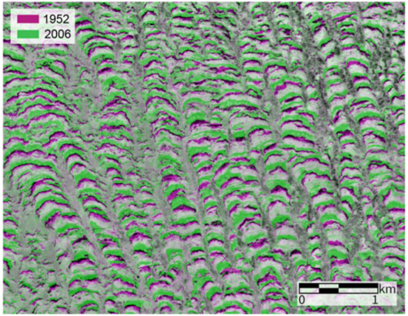
Periodic travelling waves



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

Uphill movement in ecology

Timeseries data.[5]

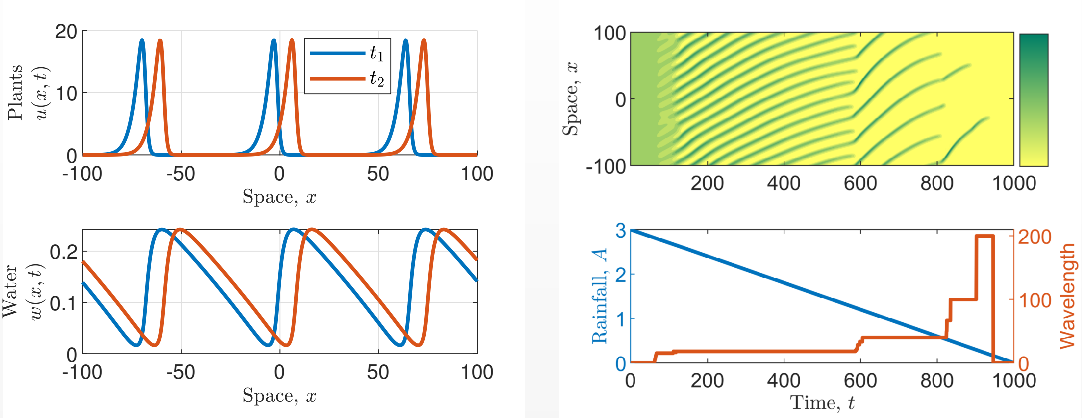


Uphill migration due to water gradient.[6]

- Data shows that vegetation stripes can move uphill ($< 1m$ per year).
- No data on mussel band movement due to destruction during winter storms.

[5] Gandhi, P. et al.: *Dryland ecohydrology*. Springer International Publishing, 2019, pp. 469–509.
[6] Dunkerley, D.: *Desert* 23.2 (2018).

Periodic travelling waves

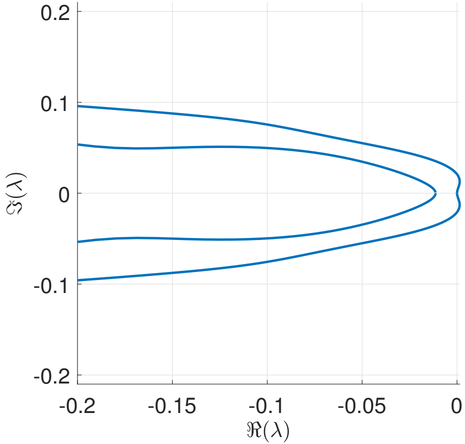


- Model represents vegetation patterns as periodic travelling waves (PTWs).
- Along rainfall gradient, transition from uniform vegetation to desert occurs via several pattern transitions.

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.[a]

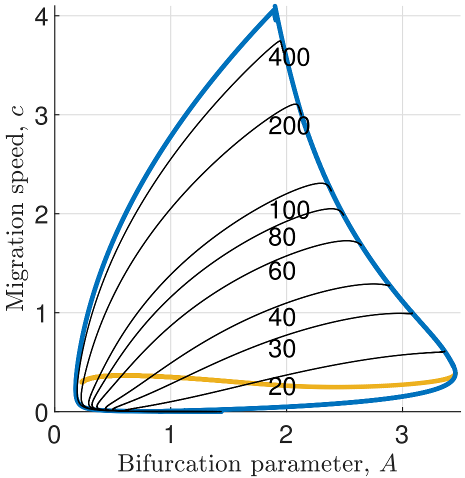
[a] Rademacher, J. D., Sandstede, B. and Scheel, A.: *Physica D* 229.2 (2007).



Wavelength changes

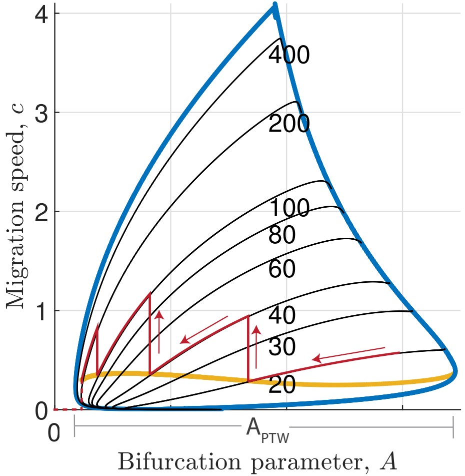
- State-of-the-art: predict wavelength changes through PTW stability properties.
- PTW linear stability is determined by their essential spectra.
- Calculated using numerical continuation.[a]
- Wavelengths changes are typically predicted through the *Busse balloon*: parameter space of stable PTWs.

[a] Rademacher, J. D., Sandstede, B. and Scheel, A.: *Physica D* 229.2 (2007).

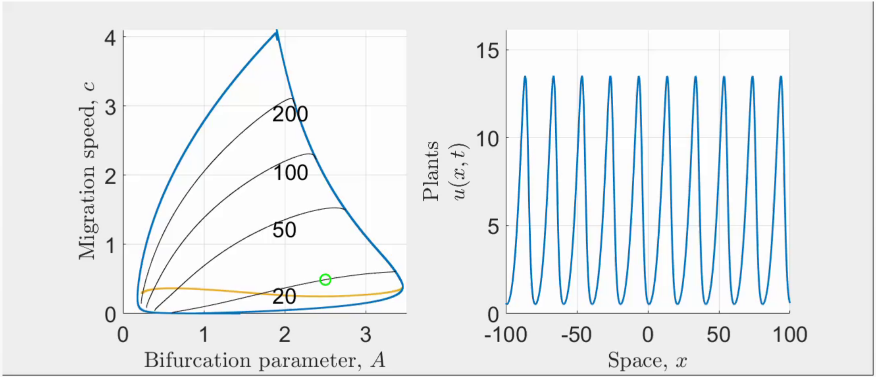


Wavelength changes

- Wavelengths changes are typically predicted through the *Busse balloon*: parameter space of stable PTWs.
- Wavelengths are preserved, provided they remain stable.
- Upon destabilisation a wavelength change occurs.



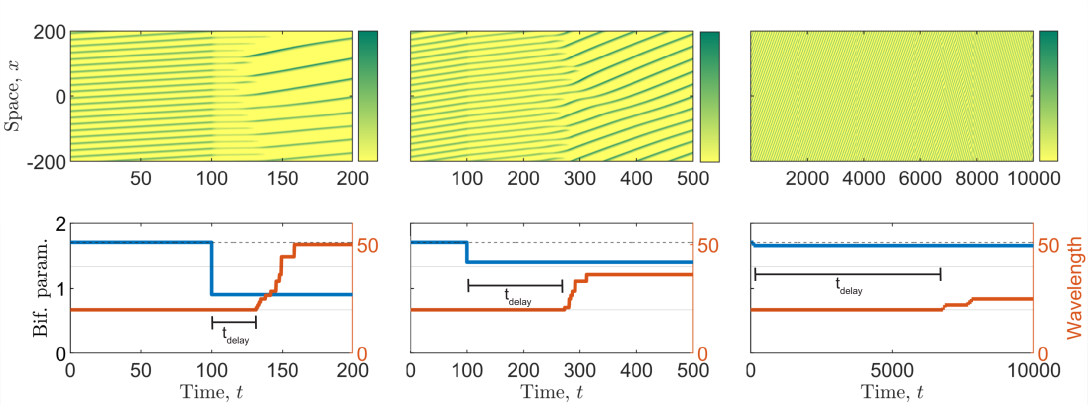
Wavelength changes



alternative video link.

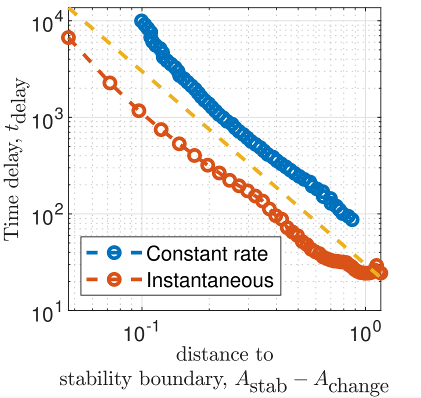
- Significant delays between crossing a stability boundary and observing wavelength changes occur.

Delays to wavelength changes



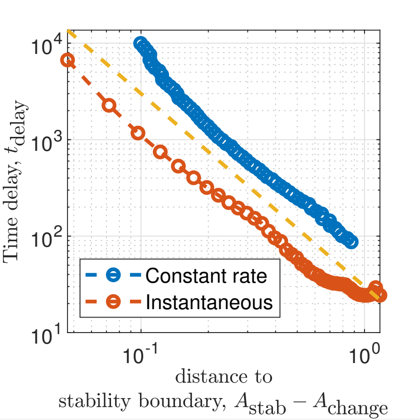
- Significant delays between crossing a stability boundary and observing wavelength changes occur.
- Order of magnitude differences in delay depending on parameter values.

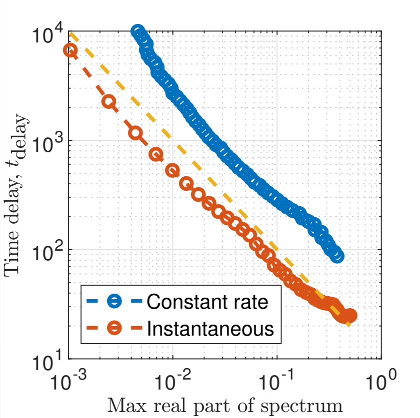
Predicting delays



There are clear trends between delay and bifurcation parameter

Predicting delays





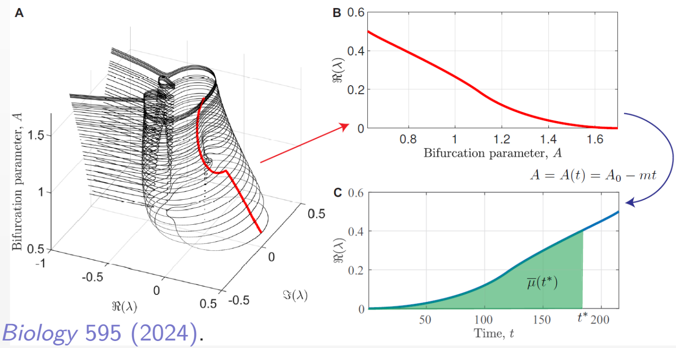
There are clear trends between delay and bifurcation parameter and delay and max real part of the spectrum. no predictive power

Predicting delays

Can predict the order of magnitude of the delay through the accumulated maximal instability[7]

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

t_{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.



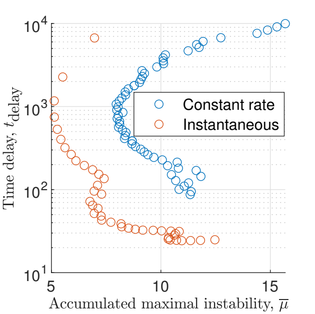
[7] EL and Sensi, M.: *Journal of Theoretical Biology* 595 (2024).

Predicting delays

Can predict the order of magnitude of the delay through the accumulated maximal instability[7]

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

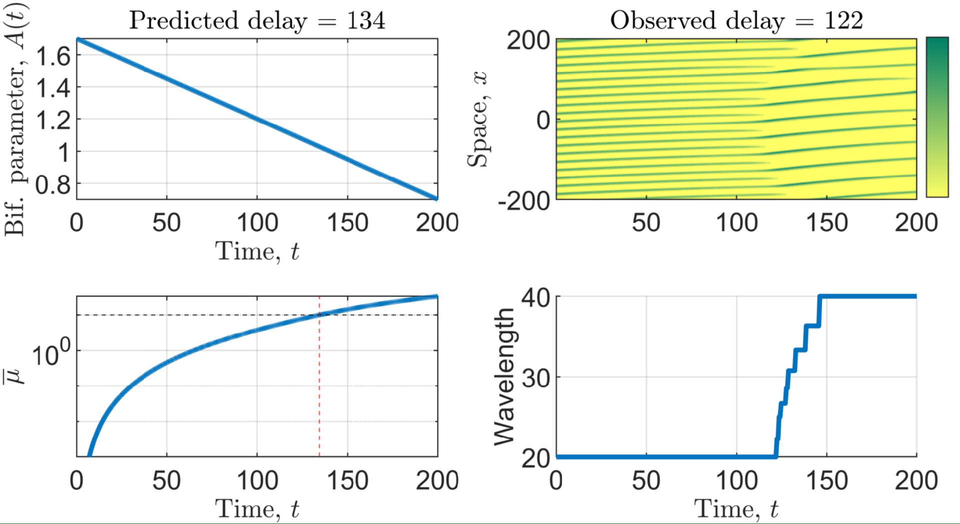
t_{stab} is the time of the last crossing of the stability boundary.
$\mu(t)$ is the max real part of the spectrum at time t.



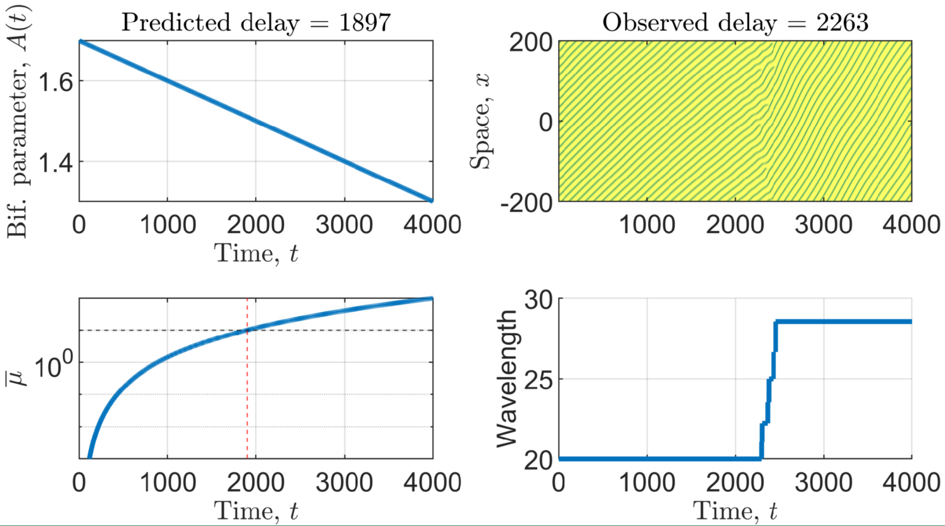
Wavelength change occurs when $\overline{\mu} \approx 10$

[7] EL and Sensi, M.: *Journal of Theoretical Biology* 595 (2024).

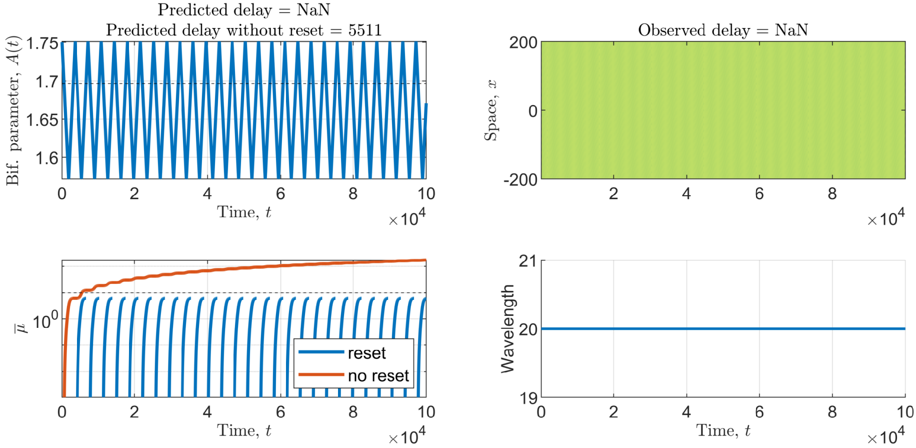
Delay prediction in practice



Delay prediction in practice

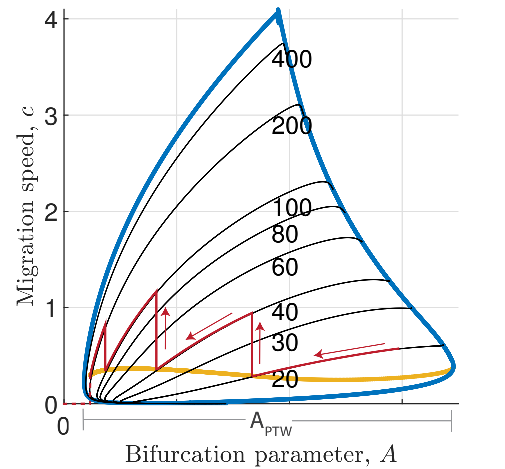


Delay prediction reset in stable regions



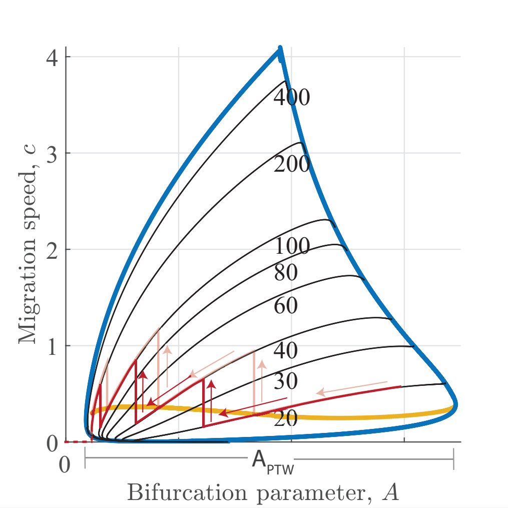
Conclusions

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



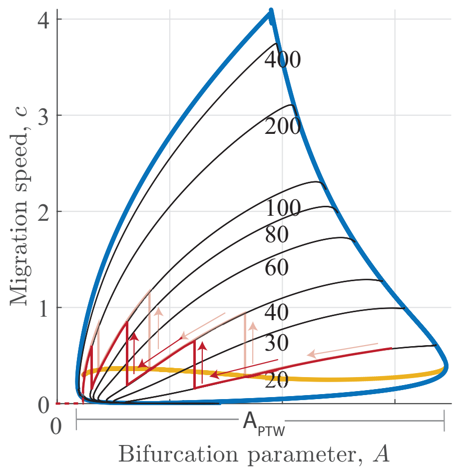
Conclusions

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



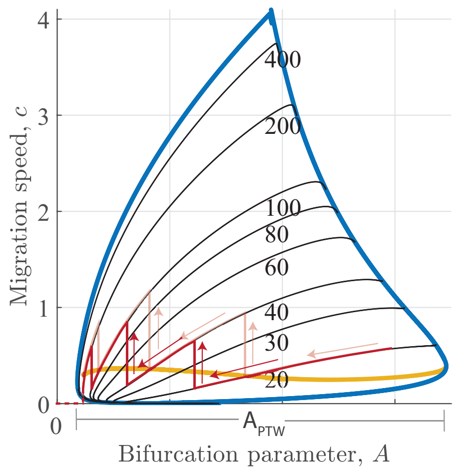
Conclusions

- 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?



References

Slides are available on my website.

`http://lukaseigentler.github.io`

[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.