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<http://lukaseigentler.github.io>

Can we predict wavelength changes of banded vegetation patterns?

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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

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

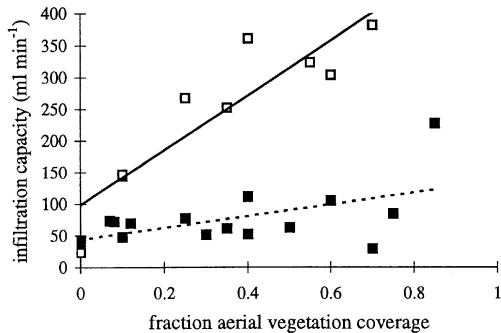
¹Klausmeier, C. A.: *Science* 284.5421 (1999).

Klausmeier model for vegetation patterns

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 \end{aligned}$$

Water uptake



Infiltration capacity increases with plant density²

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

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.

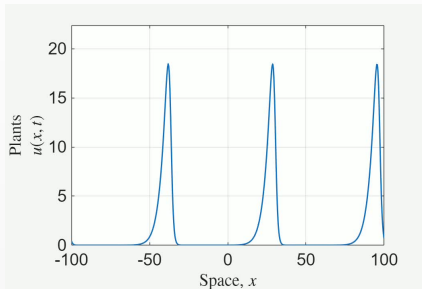
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Periodic travelling waves

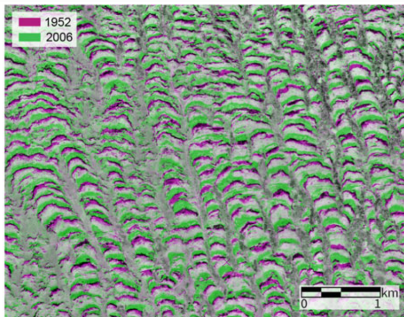


alternative video link.

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

Uphill movement in ecology

Timeseries data.⁴



Uphill migration due to water gradient.⁵

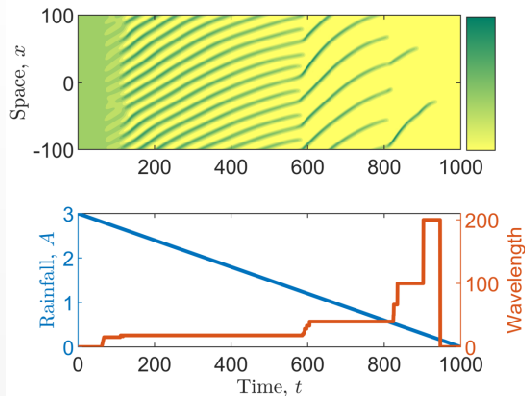
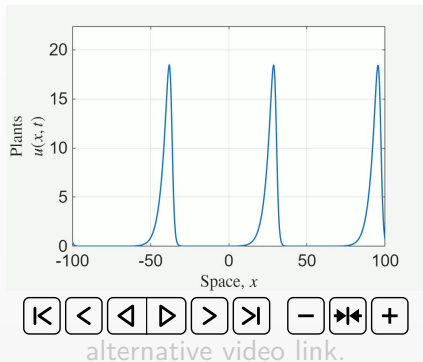


- Data shows that vegetation stripes can **move uphill** ($< 1m$ per year).

⁴Gandhi, P. et al.: *Dryland ecohydrology*. Springer International Publishing, 2019, pp. 469–509.

⁵Dunkerley, D.: *Desert 23.2* (2018).

Periodic travelling waves

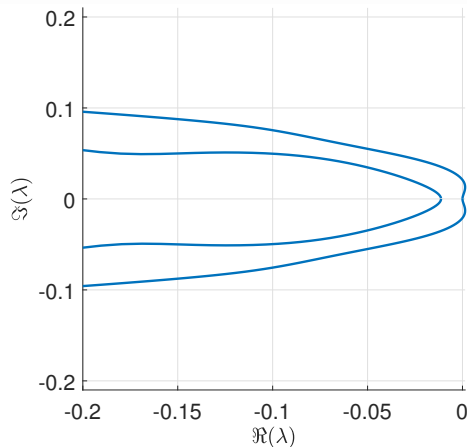


- Model represents vegetation patterns as **periodic travelling waves (PTWs)**.
- Along rainfall gradient, transition from uniform vegetation to desert occurs via several pattern transitions.

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

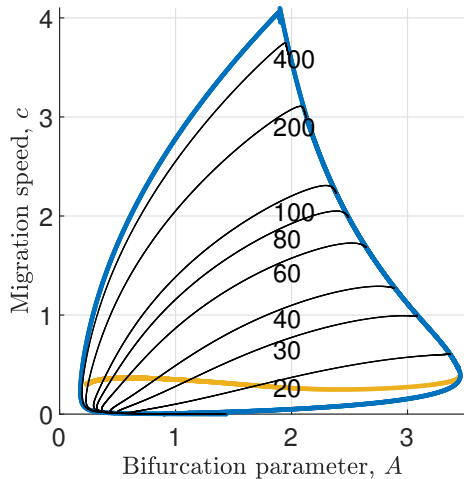
^aRademacher, J. D., Sandstede, B. and Scheel, A.: *Physica D* 229.2 (2007).



Wavelength changes

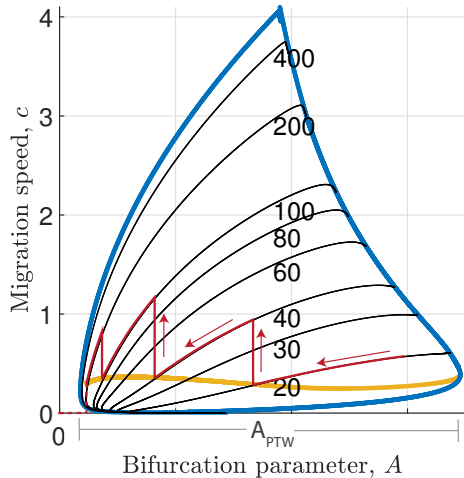
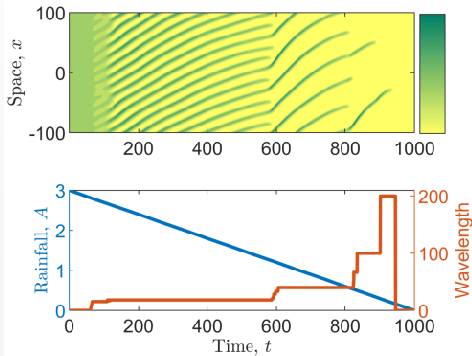
- State-of-the-art: predict wavelength changes through PTW stability properties.
- PTW linear stability is determined by their **essential spectra**.
- Calculated using numerical continuation.^a
- Wavelengths changes are typically predicted through the **Busse balloon**: parameter space of stable PTWs.

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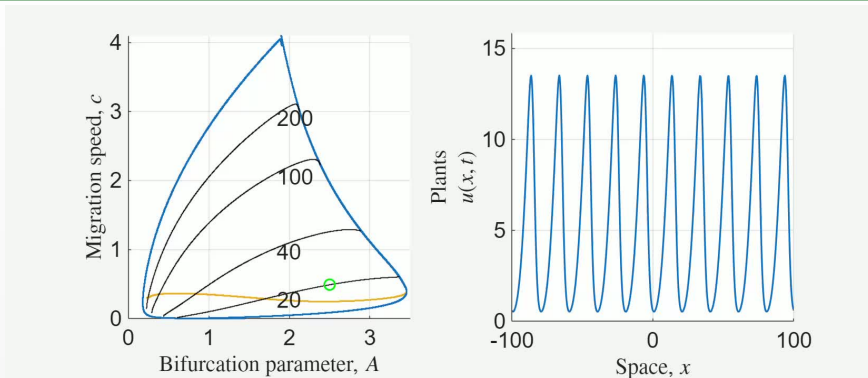


Wavelength changes

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



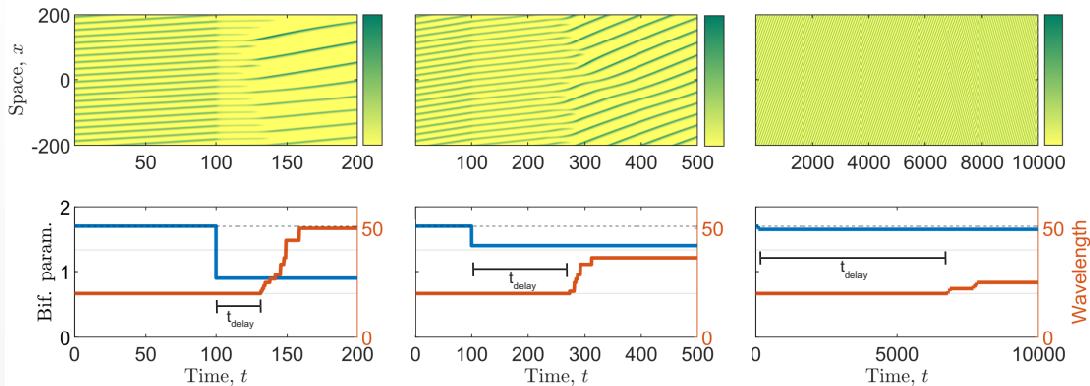
Wavelength changes



[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.

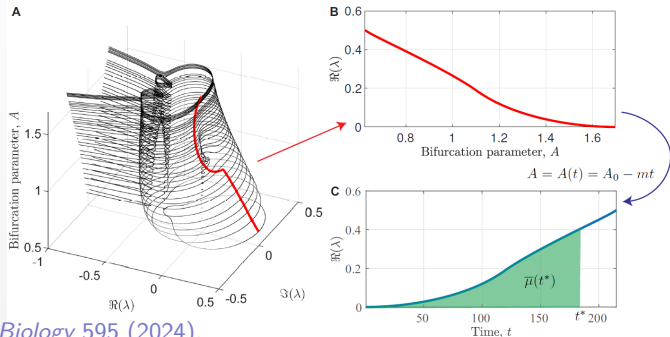
Predicting delays

Can predict the **order of magnitude of the delay** through the **accumulated maximal instability**⁶

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

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 .



⁶EL and Sensi, M.: *Journal of Theoretical Biology* 595 (2024).

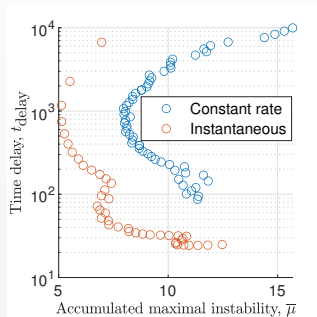
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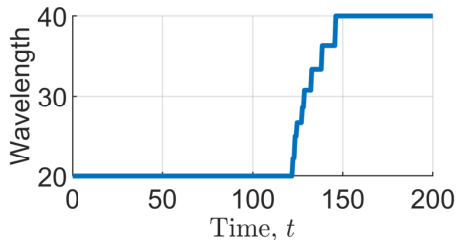
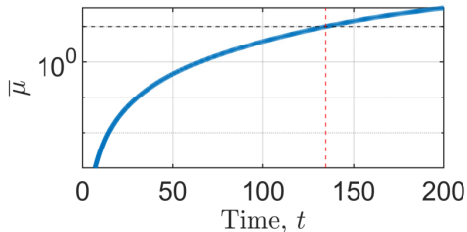
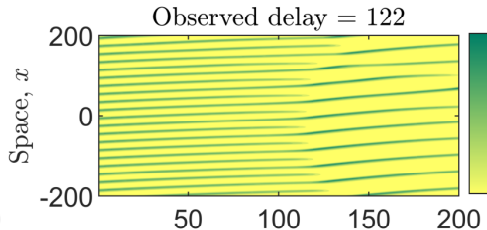
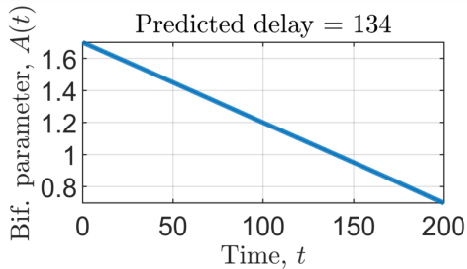
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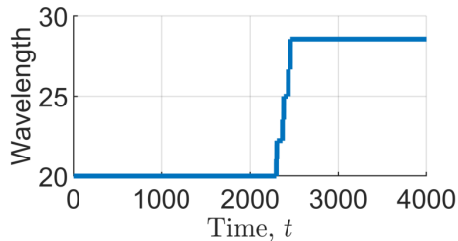
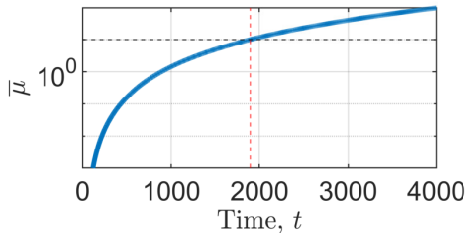
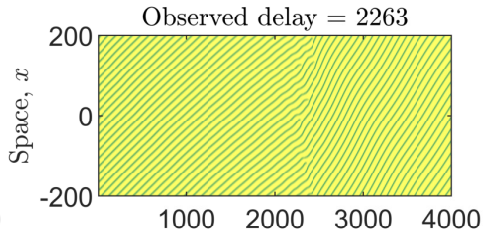
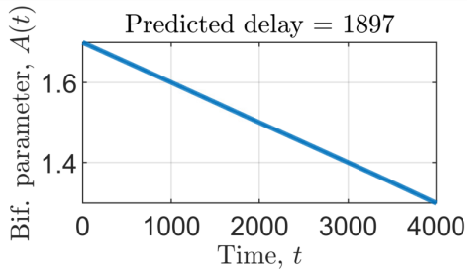
Wavelength change occurs when $\bar{\mu} \approx 10$

⁶EL and Sensi, M.: *Journal of Theoretical Biology* 595 (2024).

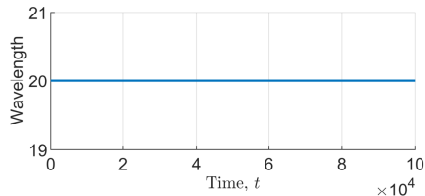
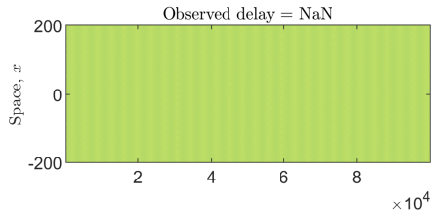
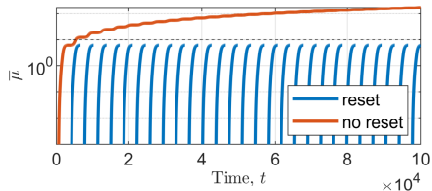
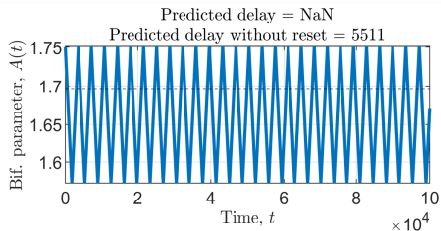
Delay prediction in practice



Delay prediction in practice

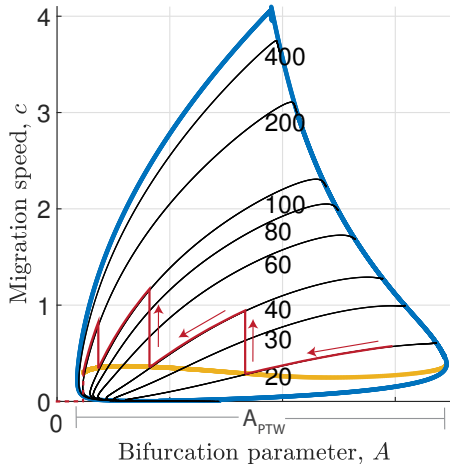


Delay prediction reset in stable regions



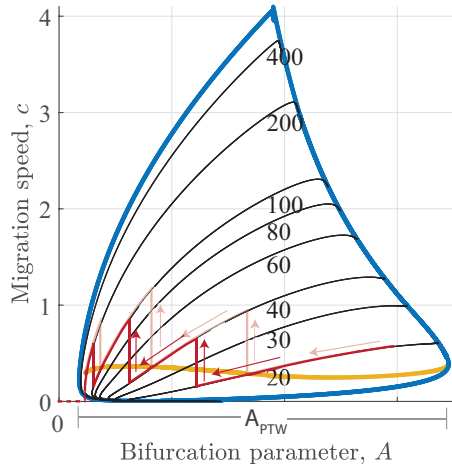
Conclusions

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



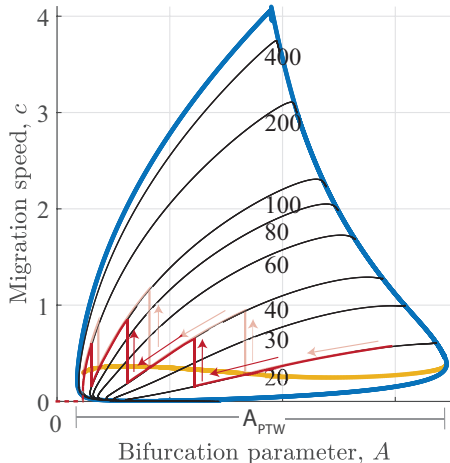
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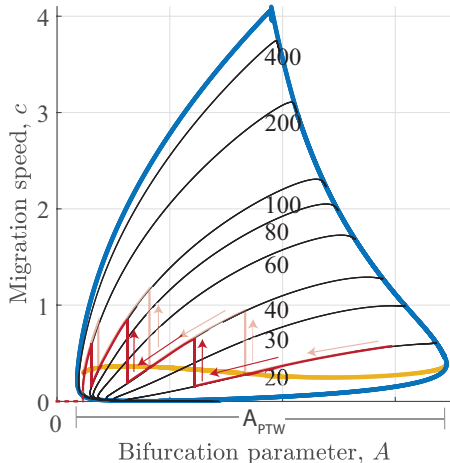
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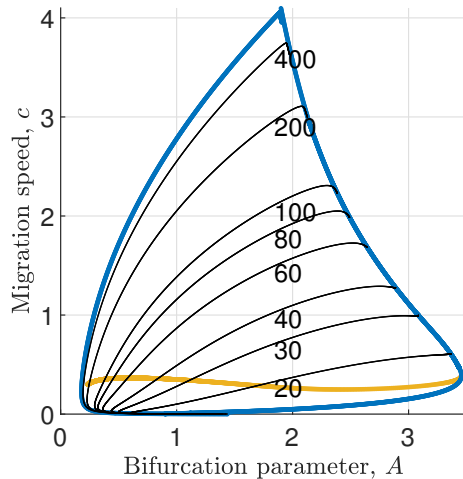
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- Order of magnitude of the delay can be predicted by tracking the maximum real part of the spectrum of the destabilised pattern over time.
- Open question: What new wavelength is chosen?



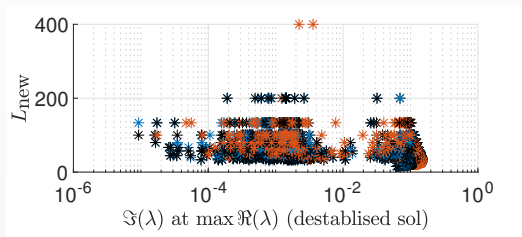
Wavelength changes

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



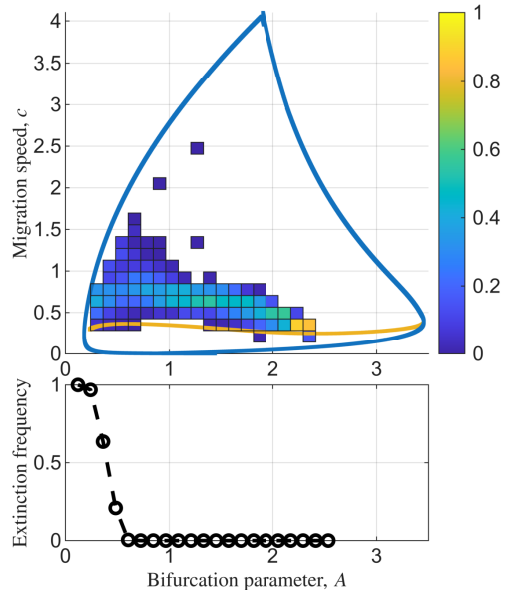
Linear analysis insufficient

- 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?

- What (new) methods do we need to understand periodic travelling wave wavelength selection?
- Similar trends observed for mussel model $\Rightarrow$ is it possible to derive principles applicable to a wider class of models?
- Do we have empirical evidence of wavelength changes in dryland vegetation patterns?

References

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- [1] Eigentler, L. and Sensi, M.: 'Wavelength selection for periodic travelling waves: an unsolved problem'. *Bull. Math. Biol.* (in press).
- [2] 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.