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

Pattern migration (or not?) of dryland vegetation stripes

MODIS, ICMS

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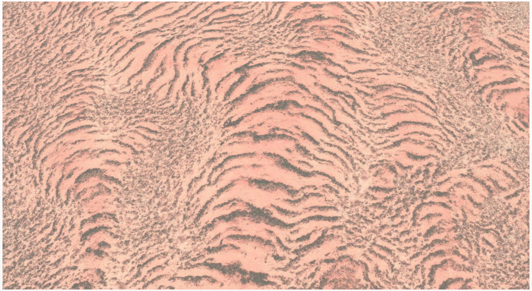
joint work with Jonathan A Sherratt (Heriot-Watt Univ.)

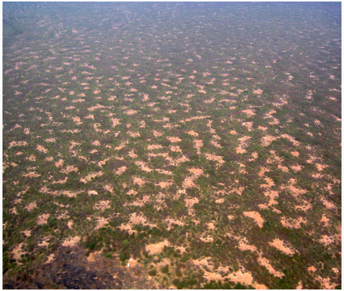
Vegetation patterns

Vegetation patterns are a classic example of a self-organisation principle in ecology.

Stripe pattern in Ethiopia[1].



Gap pattern in Niger[2].

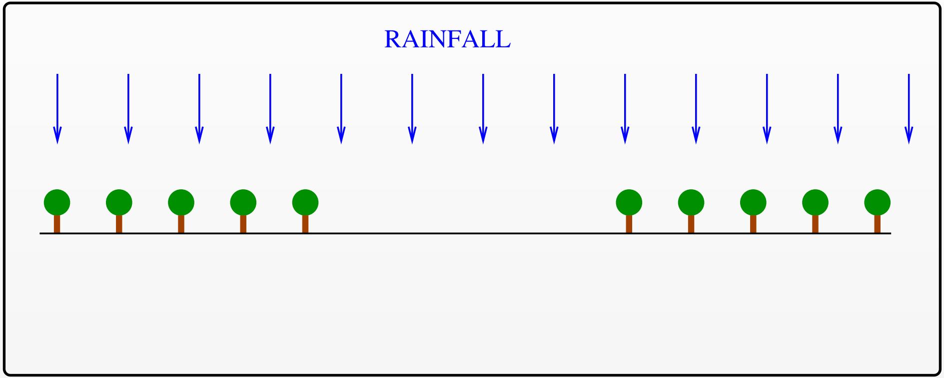


- Plants increase water infiltration into the soil and thus induce a positive feedback loop.

[1]Source: Google Maps
[2]Source: Wikimedia Commons

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.



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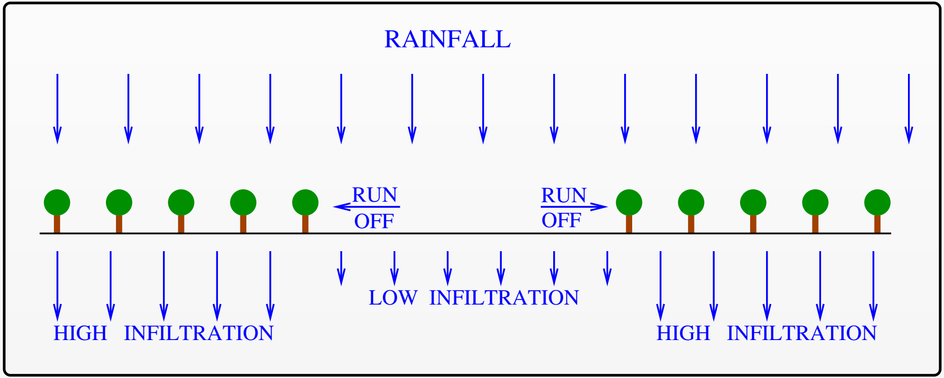

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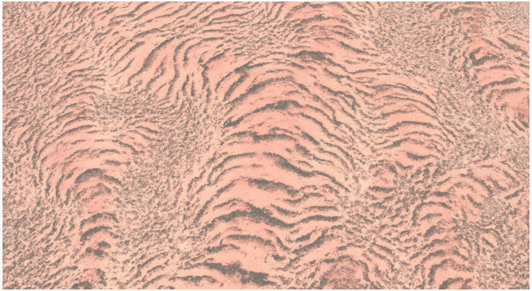
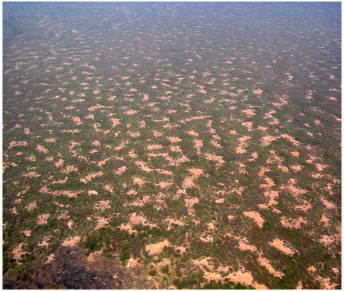


Gap pattern in Niger[4].



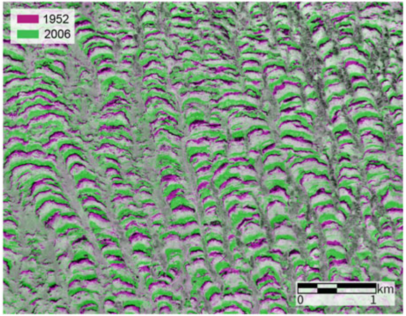
- On sloped ground, stripes grow parallel to the contours.

[3]Source: Google Maps

[4]Source: Wikimedia Commons

Vegetation patterns

Timeseries data.[5]



Uphill migration due to water gradient.[6]

- Contrasting field data: stripes either move uphill ($< 1m$ per year) or are stationary[7].
- No reports of downhill movement.

[5] Gandhi, P. et al.: *Dryland ecohydrology*. Springer International Publishing, 2019, pp. 469–509.
[6] Dunkerley, D.: *Desert* 23.2 (2018).
[7] Deblauwe, V. et al.: *Ecol. Monogr.* 82.1 (2012).

Klausmeier model

One of the most basic phenomenological models is the extended Klausmeier reaction-advection-diffusion model.[8]

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

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

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

Klausmeier model

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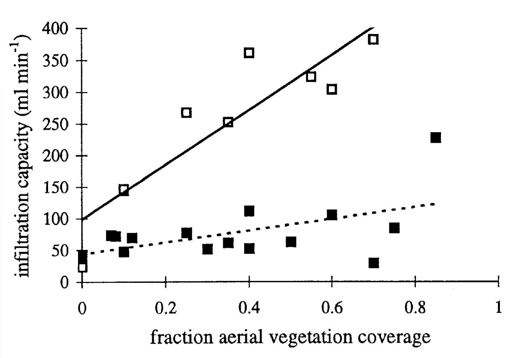
\end{aligned}$$

Water uptake



Infiltration capacity increases with plant density[9]

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

$\Rightarrow$Water uptake = Water density x plant density x infiltration rate.

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

Research question

- How can the contrasting field data on uphill movement be explained?

Main research question

- How does nonlocal seed dispersal affect onset, existence and stability of patterns?
  $\Rightarrow$ How can the contrasting field data on uphill movement be explained?

Local Model

The Klausmeier model models plant dispersal by a diffusion term, i.e. a local process.

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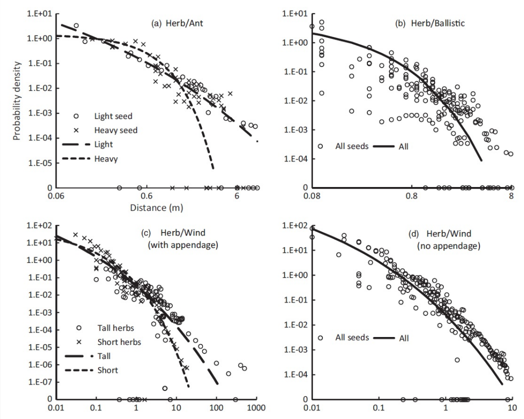
\end{aligned}
$$

Nonlocal seed dispersal



Data of long range seed dispersal [10]

More realistic: Include effects of nonlocal processes, such as dispersal by wind or large mammals.

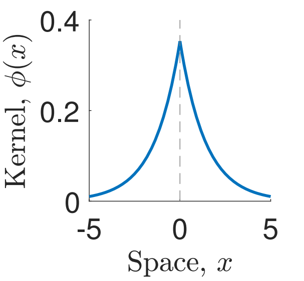
[10] Bullock, J. M. et al.: *J. Ecol.* 105.1 (2017)

Nonlocal model

Diffusion is replaced by a convolution of the plant density u with a dispersal kernel ϕ. The scale parameter a controls the width of the kernel.

$$\frac{\partial u}{\partial t} = \overbrace{u^2 w}^{\text{plant growth}} - \overbrace{Bu}^{\text{plant loss}} + \overbrace{C\left(\phi(\cdot;a) * u(\cdot,t) - u\right)}^{\text{nonlocal plant dispersal}},$$

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



Laplacian kernel

If ϕ decays exponentially as $|x| \to \infty$, and $C = 2/\sigma(a)^2$, then the nonlocal model tends to the local model as $\sigma(a) \to 0$.
E.g. Laplace kernel

$$\phi(x) = \frac{a}{2} e^{-a|x|}, \quad a > 0, \quad x \in \mathbb{R}.$$

Useful because

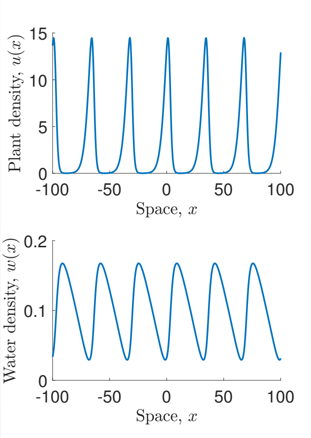
$$\widehat{\phi}(k) = \frac{a^2}{a^2 + k^2}, \quad k \in \mathbb{R}.$$

and allows transformation into a local model. If $v(x,t) = \phi(\cdot; a) * u(\cdot; t)$, then

$$\frac{\partial^2 v}{\partial x^2}(x,t) = a^2 (v(x,t) - u(x,t))$$

Travelling waves

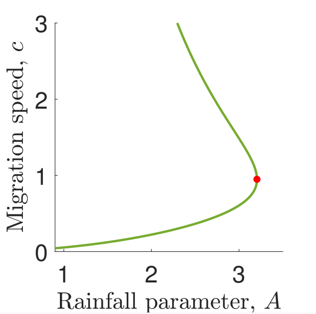
- Numerical simulations of the model on sloped terrain suggest uphill movement $\Rightarrow$ Periodic travelling waves.
- Patterns correspond to limit cycles of the travelling wave integro-ODEs.



Numerical simulation.

Travelling waves

- Numerical simulations of the model on sloped terrain suggest uphill movement $\Rightarrow$ Periodic travelling waves.
- Patterns correspond to limit cycles of the travelling wave integro-ODEs.
- Numerical continuation shows that patterns emanate from a Hopf bifurcation and terminate at a homoclinic orbit.
- In the PDE model, pattern onset occurs at a threshold $A = A_{\text{max}}$, the maximum rainfall level of the Hopf bifurcation loci in the travelling wave ODEs.



Location of the Hopf bifurcation in A-c plane.

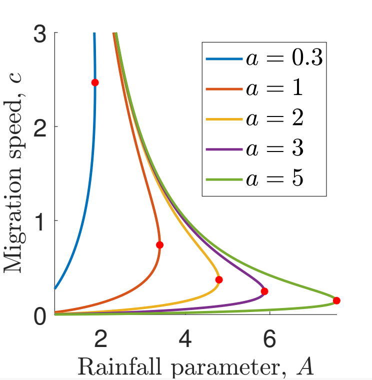
Pattern onset

Using that $\nu \gg 1$,

$$A_{\max} = \left(\frac{3C - B - 2\sqrt{2C}\sqrt{C-B}}{(B+C)^2}\right)^{\frac{1}{4}} a^{\frac{1}{2}} B^{\frac{5}{4}} \nu^{\frac{1}{2}},$$

to leading order in ν as $\nu \to \infty$.

- Note that $A_{\max} = O(\sqrt{\nu})$.
- Decrease in a (i.e. increase in kernel width) causes decrease of $A_{\max}$.
- Increase in dispersal rate C causes decrease of $A_{\max}$.

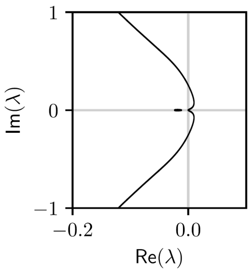


Locus of Hopf bifurcation for fixed C and varying a.[11]

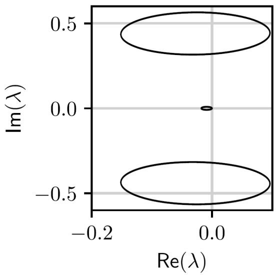
[11] EL and Sherratt, J. A.: *J. Math. Biol.* 77.3 (2018)

Pattern stability

- The essential spectrum of a periodic travelling wave determines the behaviour of small perturbations. $\Rightarrow$ Tool to determine pattern stability.
- Two different types stability boundaries: Eckhaus-type and Hopf-type.
- Essential spectra and stability boundaries are calculated using the numerical continuation method by Rademacher et al.[12]



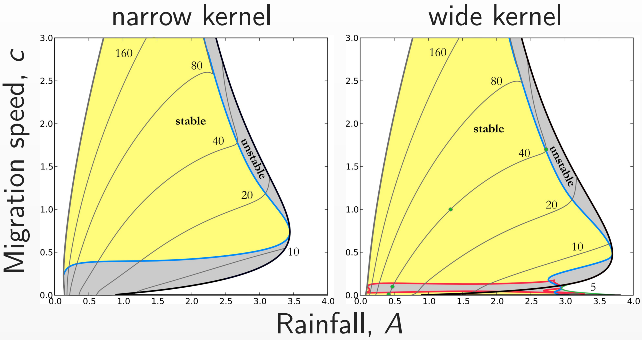
Eckhaus-type



Hopf-type

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

Pattern existence and stability



Stability of patterns in the A-c plane.[13]

For wide kernels, the stability boundary towards the desert state changes from Eckhaus to Hopf-type. This yields

- increased resilience due to oscillating vegetation densities in peaks,

[13] Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* 481 (2018)

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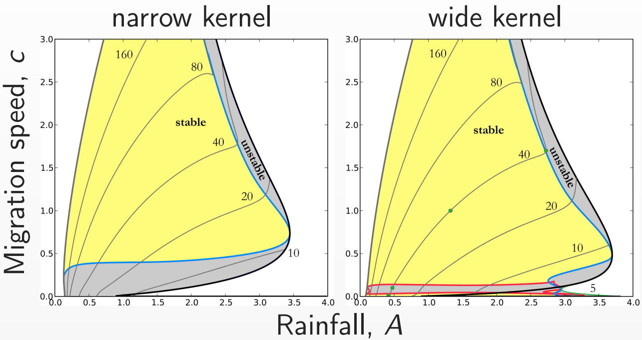
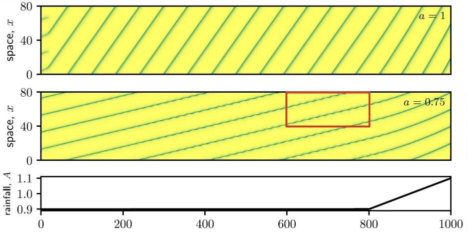


Stability of patterns in the A-c plane.[14]



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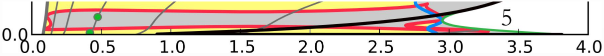
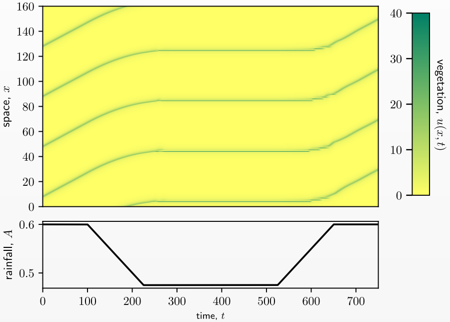
[14] Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* 481 (2018)





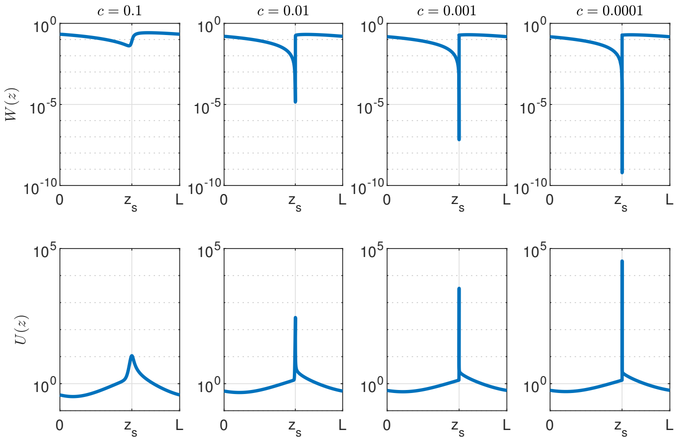
Existence of stable (almost) stationary patterns.[15]

For wide kernels, the stability boundary towards the desert state changes from Eckhaus (sideband) to Hopf-type. This yields

- increased resilience due to oscillating vegetation densities in peaks,
- existence of stable patterns with small migration speed ($c \ll 1$).

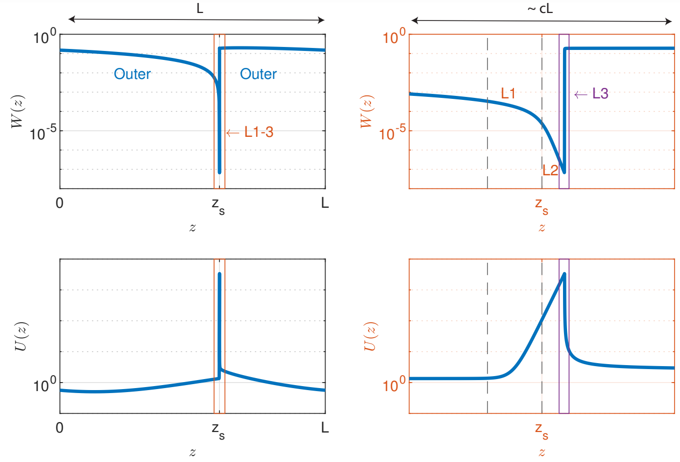
[15] Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* 481 (2018)

Almost stationary spike patterns



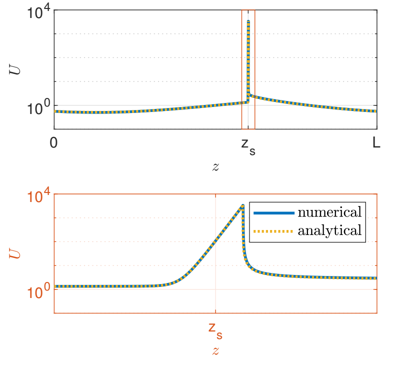
As c decreases, plant density develops a “spike”.

Almost stationary spike patterns



Layered structure of spike solution

Almost stationary spike patterns



Analytical calculation of (almost) stationary patterns.[16]

Existence of almost stationary patterns is confirmed analytically using a singular perturbation theory approach, exploiting $c \ll 1$.

[16] EL and Sherratt, J. A.: *J Math Biol* 86.15 (2023)

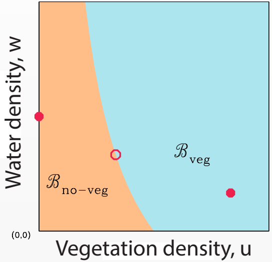
Main conclusion

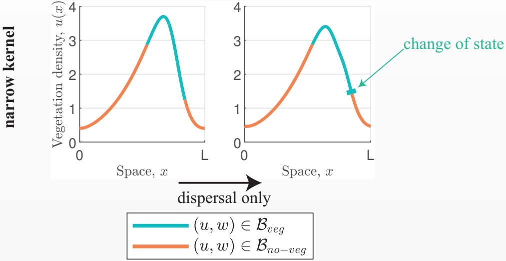
- How can the contrasting field data on uphill movement be explained?

For long seed dispersal distances moving (uphill) and stationary patterns can occur for the same parameter values.

Almost stationary patters

Q: Why do longer mean dispersal distances slow down pattern migration?





- narrow kernel: dispersal-induced plant increase at pattern edge causes transition from basin of attraction of desert state to vegetated state.

Almost stationary patters

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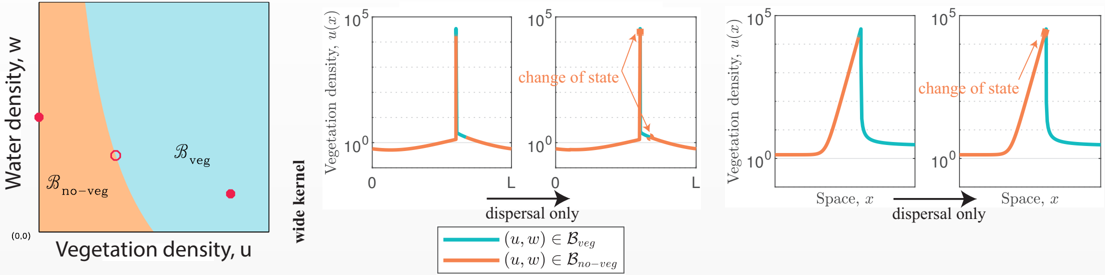

- Narrow kernel: dispersal-induced plant increase at pattern edge causes transition from basin of attraction of desert state to vegetated state.
- Wide kernel: less dispersal to stripe edges $\rightarrow$ insufficient to cause transition from basin of attraction of desert state to vegetated state.

Other conclusions

- Wider kernels and higher dispersal rates inhibit pattern onset.
- Stability analysis of periodic travelling waves provides ecological insights into pattern dynamics: Long-range seed dispersal increases the resilience of a pattern and stabilises (almost) stationary patterns.
- Numerical simulations (pattern onset) and space discretisation to avoid nonlocality (calculation of essential spectra) show no qualitative differences for other kernel functions.

Future Work

- Empirical tests of these hypotheses?
- How can a system reach a non-migration state?
- How resilient are non-migration states to environmental change?

References

Slides are available on my website.

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[1] Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* 481 (2018), pp. 151–161.

[2] Eigentler, L. and Sherratt, J. A.: *J. Math. Biol.* 77 (2018), pp. 739–763.

[3] Eigentler, L. and Sherratt, J. A.: *J. Math. Biol.* 86.15 (2023).

[4] EL and Sherratt, J. A.: *J. Math. Biol.* 77.3 (2018), pp. 739–763.