

Quasiperiodic Patterns in Biology and Elsewhere

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Talk plan

- Background
- Continuous RD systems
 - Multiple species, *D* dim.
 - Single species, one dim.
 - Patterns and Newton
 - Stability and Schrödinger nogo
- Discrete RD systems
 - Cellular networks
 - One species, one dim. lattice
 - Discrete Newton!
- Alternative dynamics: Active transport
 - Auxin example simple model
 - Same patterns, better stability
- Quasi-periodic patterns from discrete spatial Newton eq.
 - Area-preserving maps
 - Auxin patterns, quasi-periodicity and conservative maps
- Conclusions

Continuous RD – dynamics

• Multispecies, D dim: general RD eqs. for $\{u_i(\mathbf{r}, t)\}$:

 $\dot{u}_i = D_i \nabla^2 u_i + f_i(u_1, \ldots, u_n)$

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Focus on single species, one dim: u(x, t): RD eq:

$$\dot{u}=u''+U'(u)$$

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• Has a Lyapunov function S = Lagrange action, decreases!

$$S = \int \left(\frac{1}{2}u'^2 - U(u)\right) dx$$

$$\Rightarrow \dot{S} = -\int \dot{u}^2 dx \le 0$$

Stable iff local min of Lyapunov S!

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- ▶ Pattern u(x) defined by level curve of H in phase space u, u':
 - \Rightarrow typically periodic patterns:



▶ Pattern *u*(*x*) stable? Iff local min. of *S*! How know?

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$$\mathbf{H} = -\partial_x^2 + V(x)$$

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- Pattern u₀(x) stable if H positive semidef. (i.e. all eigenvalues λ ≥ 0)
- Zero mode: ε ∝ u' (sliding mode) has λ = 0!
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- Only chance if u monotonously interpolates between two deg. max of U(u)!

So no stable oscillatory patterns!

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Discrete RD – general case

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- Need discrete space version of RD dynamics
- Most general case: consider RD version for multiple species on arbitrary graph G:

$$\dot{\mathbf{u}}_i = \mathbf{D} \sum_{j \in \mathcal{N}(i)} (\mathbf{u}_j - \mathbf{u}_i) - \mathbf{f}(\mathbf{u})$$

where $\mathcal{N}(i)$ defines the set of neighbor nodes of node *i*.

Discrete RD - one species, one dimension

► Again, focus on one species on a linear one-dim. lattice, described by {u_i(t)}.

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- Dynamics: one-dim. discrete RD (rescaled units):

 $\dot{u}=u_++u_--f(u)$

in simplified notation, where u_{-} , u, u_{+} are short for u_{i-1} , u_i , u_{i+1} .

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- Properties similar to continuous case:
 - Lyapunov: $S = \sum (-uu_+ + F(u))$, with F' = f
 - Stat. sol's, patterns stable if local minima of S.

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- So no-go?

Can get similar static eqs., with an improved stability!

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 - more complicated dynamics
 - with passive diffusion as in RD, but with
 - active transport replacing the local reaction term,
 - feat. (dep. on version) e.g. matter conservation, scaling, and other nice properties.

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- Discrete space dynamics modelled with
 - more complicated dynamics
 - with passive diffusion as in RD, but with
 - active transport replacing the local reaction term,
 - feat. (dep. on version) e.g. matter conservation, scaling, and other nice properties.
- Written out in its full glory, the simplest auxin model dynamics reads:

$$\dot{u} = D(u_{+} - 2u + u_{-}) + T\left(\frac{uu_{+}}{u_{++} + u} - u + \frac{uu_{-}}{u_{+} + u_{--}}\right)$$

where D and T are parameters governing the rate of diffusive and active transport, respectively.

Auxin model – continued

More compactly, the auxin dynamics can be written as a continuity eqn.:

$$\dot{u} = -\Delta_+ I = -\Delta_+ u u_- \Delta_- \left(\frac{D}{u} - \frac{T}{u_+ + u_-} \right),$$

where Δ_{\pm} are the local difference operators, while *I* is the flux between neighbor cells.

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- Note linearity of eqs. \Rightarrow can rescale solutions.
- Pattern eqs. follow from I = 0:

$$\frac{D}{u} - \frac{T}{u_+ + u_-} = -C$$

where *C* is a positive integration constant.

Example - auxin model

Miracle 1: the auxin pattern eq. can be turned around to yield a discrete Newton type pattern eq. with a simple, rational f(u), here given by:

$$f(u)=\frac{2u}{\mu+Ku}$$

where $\mu \in [0, 1] = 2D/T$ gives the relative balance between passive and active transport, while K > 0 is a mere rescaling of C.

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▶ By rescaling u, K can be rescaled to an arbitrary number, suitably chosen as $1 - \mu$, yielding the auxin pattern eqs. in the standard version:

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► This eq. will turn out to have some **unusual properties**!

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 $v = u_{-}$ we get

$$\begin{cases} u_+ = f(u) - v, \\ v_+ = u, \end{cases}$$

with a Jacobian **J** having a unit determinant, det J = 1!

- ► Continuous Newton eqs. define area-preserving flows in phase space u(x), u'(x).
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- Natural to study discrete Newton patterns in the u, v "phase" plane!
- Continuous Newton flows are conservative: H(u, u') = const.
- Discrete Newtonian patterns normally are not conservative!

Typical auxin model patterns in the first quadrant of the u, v plane rotate around the (1,1) fixed point (a center), and bounce off the (0,0) one (a saddle).



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Compare to the **chaotic** trajectories of a generic, nonintegrable Newton eqs. in u, vplane:



Suspect conserved quantity H(u, v) in u, v plane,

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Should follow from Newton eq. – rewrite this as

 $u_{+}^{2}g(u) - u_{+}f(u)g(u) + h(u) = u_{-}^{2}g(u) - u_{-}f(u)g(u) + h(u)$

with arbitrary g, h – and identify:

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• *H* symmetric, finally \Rightarrow *H* must be **biquadratic**:

 $H(u, v) = Au^{2}v^{2} - Buv(u+v) + C(u^{2}+v^{2}) + Duv - E(u+v) + F$

Auxin map conservative?

Working backwards from general conserved H(u, v): f must be broken quadratic:

$$f(u) = \frac{Bu^2 - Du + E}{Au^2 - Bu + C}$$

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▶ ... but multiplying upstairs/downstairs by $(1 - \mu)u - (2 + \mu)$ helps! (Miracle nr 2!)

$$f(u) = \frac{2(1-\mu)u^2 - 2(2+\mu)u}{(1-\mu)^2u^2 - 2(1-\mu)u - \mu(2+\mu)}$$

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... smooth, non-chaotic patterns!





 Discrete Newtonian systems: rich structure, lots of well-known eqs. (Newton, Schrödinger,...) – can reuse old intuition.

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- Active transport helps stability of Newtonian patterns.
- Unexpected spatial conservation law in auxin system.
- Q: What with higher dim.? Similar special properties for certain choices of reaction term? Applications in astronomy?
- Extra take-home lesson: Be careful when simulating one-dim. Newton eqs: conservation law spoilt, except for a special integrable class of f!

That's all, folks!

THANK YOU!





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