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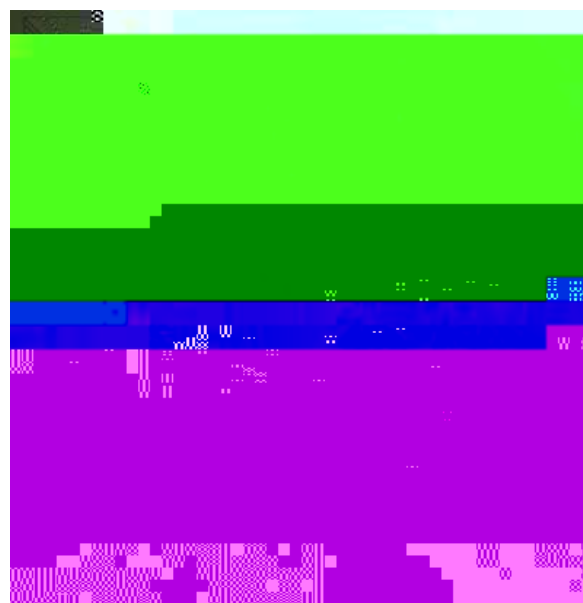
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Revealing new dynamical patterns in a reaction-
diffusion model with cyclic competition via a
novel computational framework

by

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A notable example is the Lotka-Volterra competition model in space. This model is well known in the literature with numerous applications in mathematical biology and areas of game theory such as voting models [8, 31, 34, 2, 12, 14]. In particular, this system is often considered as a paradigm for biodiversity modelling. New types of patterns have been recently demonstrated in this system which occur for spatially homogeneous diffusion coefficients [2, 31, 14]. This includes, for example, patchy invasion (the spread of a species via the formation and propagation of chaotic patches without a smooth population front), which was originally believed to occur only in predator-prey or inhibitor-activator types models [39]. Surprisingly enough, the Lotka-Volterra system still remains poorly understood, especially when the interacting species diffuse at different rates. Here, we show the existence of several new dynamical patterns, related to the spread of travelling waves, which have been missed in the literature so far, and which may have important biological applications. In particular, we demonstrate spreading patterns exhibiting complex regular spatial structure which have not been observed so far in reaction-diffusion models with a non-transitive competition such as the Lotka-Volterra cyclic model.

Note that another important gap in our knowledge about patterns and waves in reaction-diffusion models is that most existing results have been obtained for either one or two dimensions

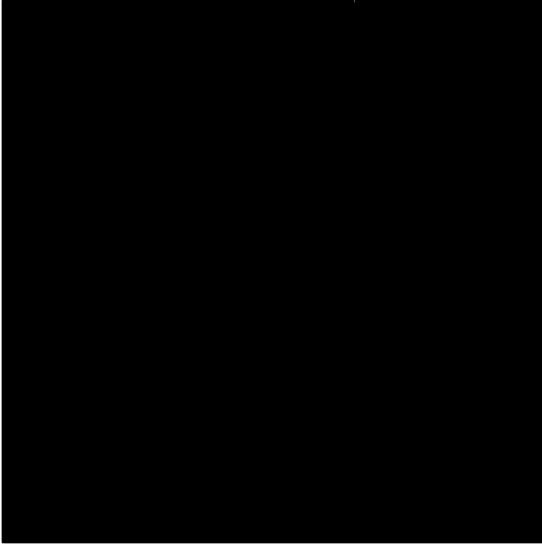
second order Crank-Nicolson Adams-Bashforth implicit-explicit (IMEX) discretisation in time, allowing us to treat the linear part of the differential operator implicitly while the nonlinear reaction term is treated explicitly. The resulting scheme therefore allows us to efficiently explore the spatio-temporal patterns arising in the Lotka-Volterra cyclic competition model in both two and three spatial dimensions. We demonstrate its effectiveness by revealing several novel

1. Such cyclic dominance is analogous to the popular game of 'rock-paper-scissors'. Some well-known examples of cyclic interactions observed in nature include competition between side-blotched lizards [45], coral reef invertebrates [9], yeast strains [37], and various bacterial strains [22]. The same model also arises in non-biological situations such as many-player prisoner's dilemma games [20] or some types of voter models [46].

Formalising the above characterisation of cyclic competition can be tricky, although here we will follow the definition given by [2]. This is based on considering the outcomes of pairwise interactions in an unbounded one-dimensional spatial domain (i.e. in the absence of a third species), starting from initial conditions such that the species densities at positive and negative infinity are equal to the carrying capacities for one species and zero for the other. Cyclic competition is then said to occur if the direction of the resulting travelling waves preserves the cyclic order $1 > 2 > 3 > 1$. For example, the domain occupied by species 2 at its carrying capacity level should eventually be replaced by a spreading wave of species 1. This generic definition of cyclic dominance allows two main types of local dynamics [2, 14]. In classical cyclic competition the phase portrait of each pairwise interaction should involve only one stable steady state corresponding to the presence of the stronger competitor at its carrying capacity. In this case, adding a spatial dimension to the local interaction does not reverse the outcome of the competition since the corresponding travelling wave will be directed from the domain occupied by the stronger competitor to that of the weaker competitor [21]. The mathematical conditions for this to occur are: $\alpha_{i,i+1} < 1$ and $\alpha_{i+1,i} > 1$. Under conditional cyclic competition, on the other hand, some local pairwise interactions can be bistable: both of the axial steady states (corresponding to the carrying capacities of one species and zero density for the other) are locally stable and the final outcome of the local competition will depend on the initial conditions. Mathematically, assuming bistability occurs for interactions between species 1 and 3 this means that $\alpha_{1,3} > 1$ and $\alpha_{3,1} > 1$. Adding a spatial dimension into the model with conditional cyclic competition should preserve the displacement order $1 > 2 > 3 > 1$ as in the classical cyclic competition. However, the conditional cyclic competition involves some constraints on the diffusion coefficients [5]

subdomain such that the centres of the two circles do not coincide. In the three-dimensional case, we explore using initial conditions formed by dividing the whole domain into 8 equal boxes and

and we refer to, e.g., [1, 52] for more on Sobolev and Bochner functions spaces. Multiplying by



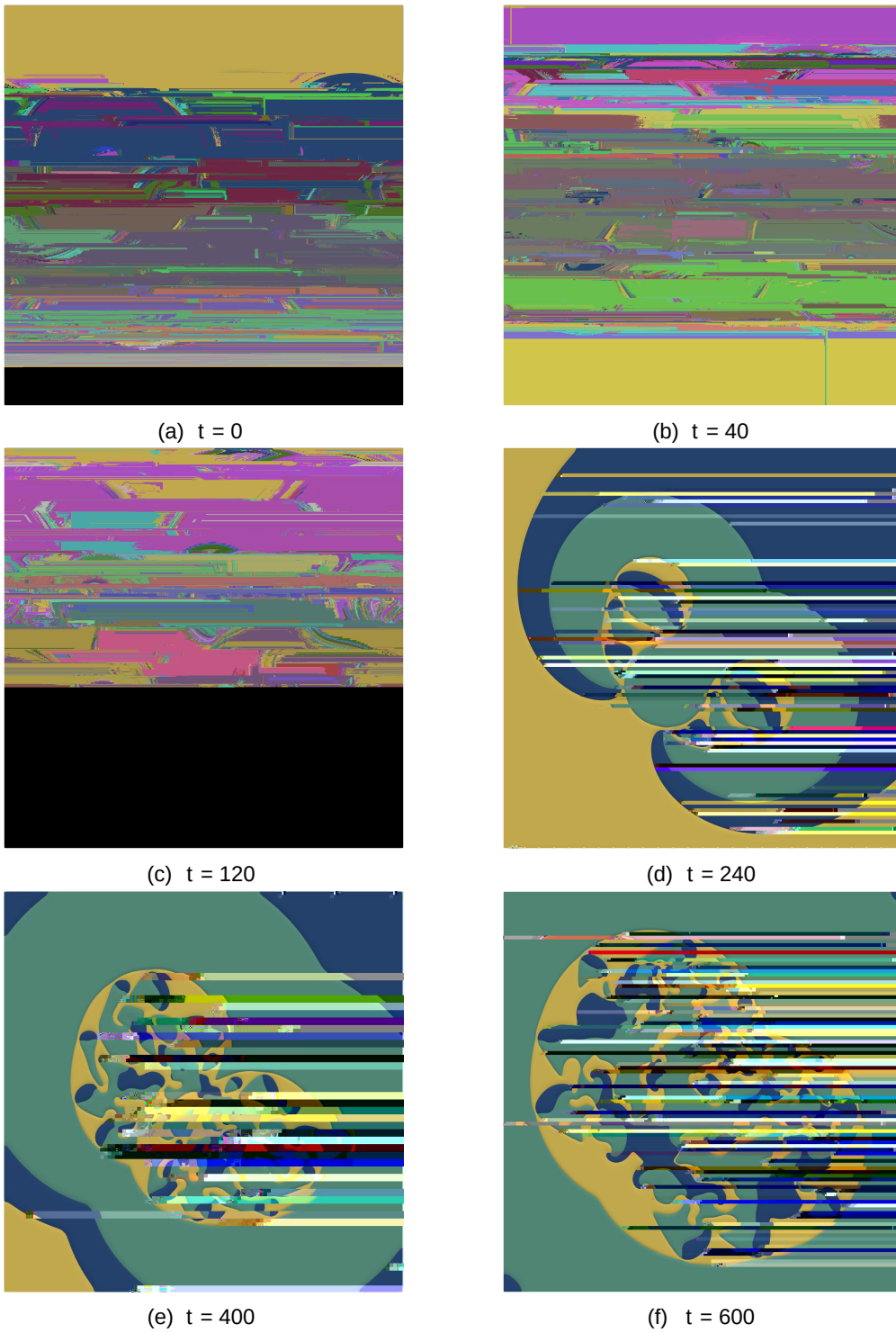
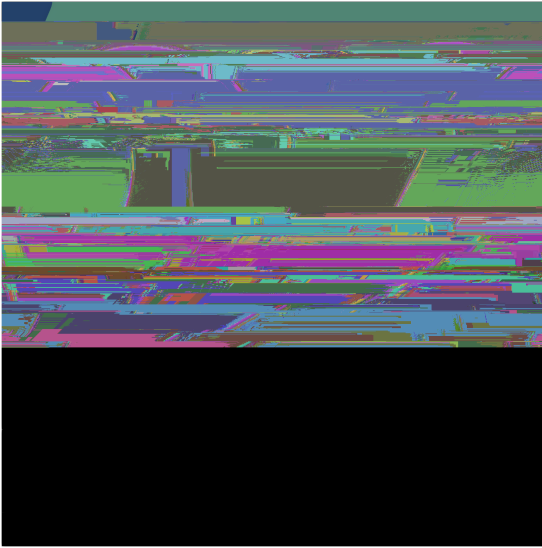


Figure 2.



domain once the bands move out of the domain. One can also see that regular droplet-like patterns travel around the edge of the chaotic domain.

The transition from the pattern of spread via droplet-like units (Fig. 1) to the one containing bands (Fig. 4) can be understood by exploring the schematic diagram shown in Fig. 5. The spread of the droplets in the wedge can be described by considering pairwise interactions of species, most of which actually occur via plane wave interactions. We can neglect the presence of a third species since the density of each species rapidly drops when entering the domain dominated by another species (except the points where all three species meet, as at the tip of the wedge). In Fig. 5, we show the direction of the spread of plane waves of cyclic displacement of species; here C_{ij} denotes the speed of the plane wave replacing species j by its stronger competitor i . One can also see a round interface between species 1 and species 2. The corresponding wave speed is denoted by $V_{1,2} = V_{1,2}(R)$, where R is the radius of the curvature. The values of C_{ij} and $V_{1,2}$ can be determined by considering the one-dimensional case (in the case of $V_{1,2}$ one should explore the system in polar coordinates). Our simulations show that for the parameters from Fig. 1, in the one-dimensional case the prorogation of a travelling pulse composed of all three species is impossible, whereas for pairwise switch waves we have $C_{1,2} > C_{2,3}$. The curvature of the wave reduces the spread of the propagation of the front of species 1 in the droplet, thus $C_{1,2} > V_{1,2}(R)$.

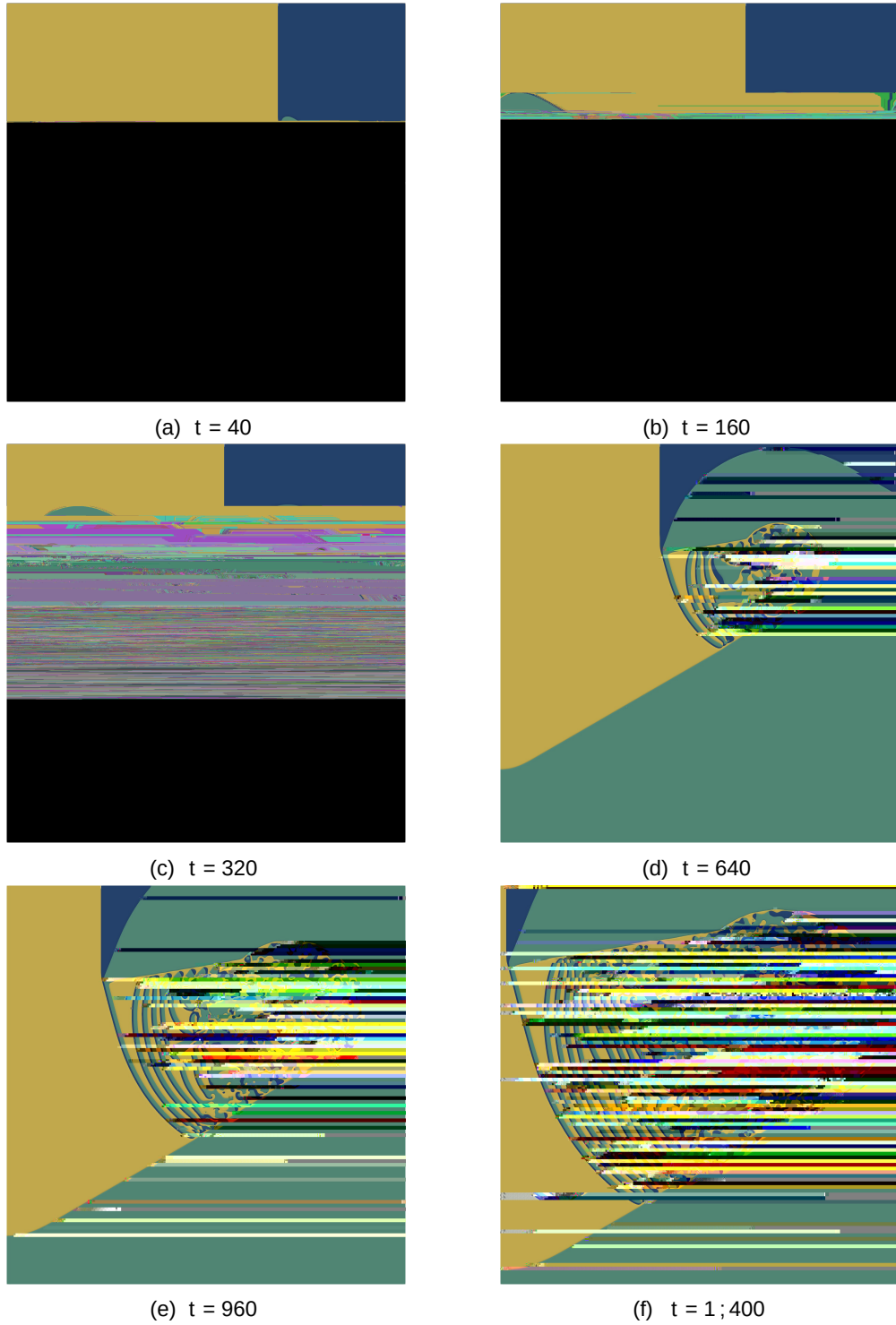


Figure 4. The evolution of the 'band' patterns which are observed when $\mathbf{r} = (1; 0; 1; 0; 9)$



Figure 5. Schematic representation of the movement of a droplet-like unit. A detailed description is given in the main text.

diffusion coefficients reveals that this pattern is robust and is observed within a 10% variation of $\alpha_2 = 0.55$ and $\alpha_3 = 0.5$.

Finally, we extend our analysis to the three-dimensional case. We focus on exploring the three-dimensional analogue of the regular droplet-like structure observed in the two-dimensional

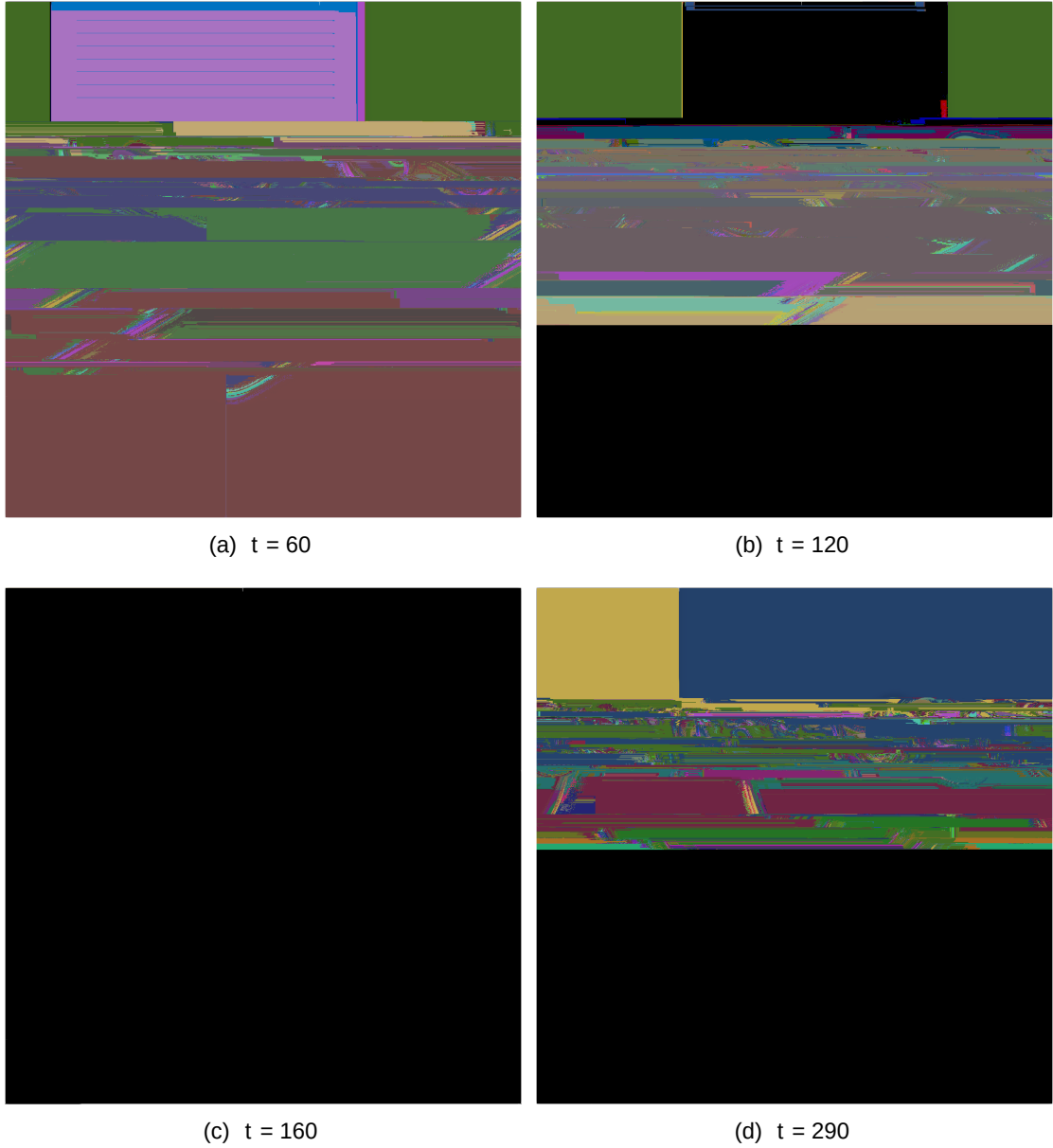


Figure 6. The evolution of the 'glider' patterns which are observed when $\alpha_2 = 0.55$ and $\alpha_3 = 0.5$, $\alpha_{3,1} = 1:3$ and the initial conditions are the same as in Fig. 1. The three colours indicate the regions of the domain in which each of the three competing species dominates.

We introduce the function $f_h : H^1(\Omega) \rightarrow V_h$ such that, for any $v \in H^1(\Omega)$,

$$(f_h(v); \phi) = (f(v); \phi) \quad \forall \phi \in V_h;$$

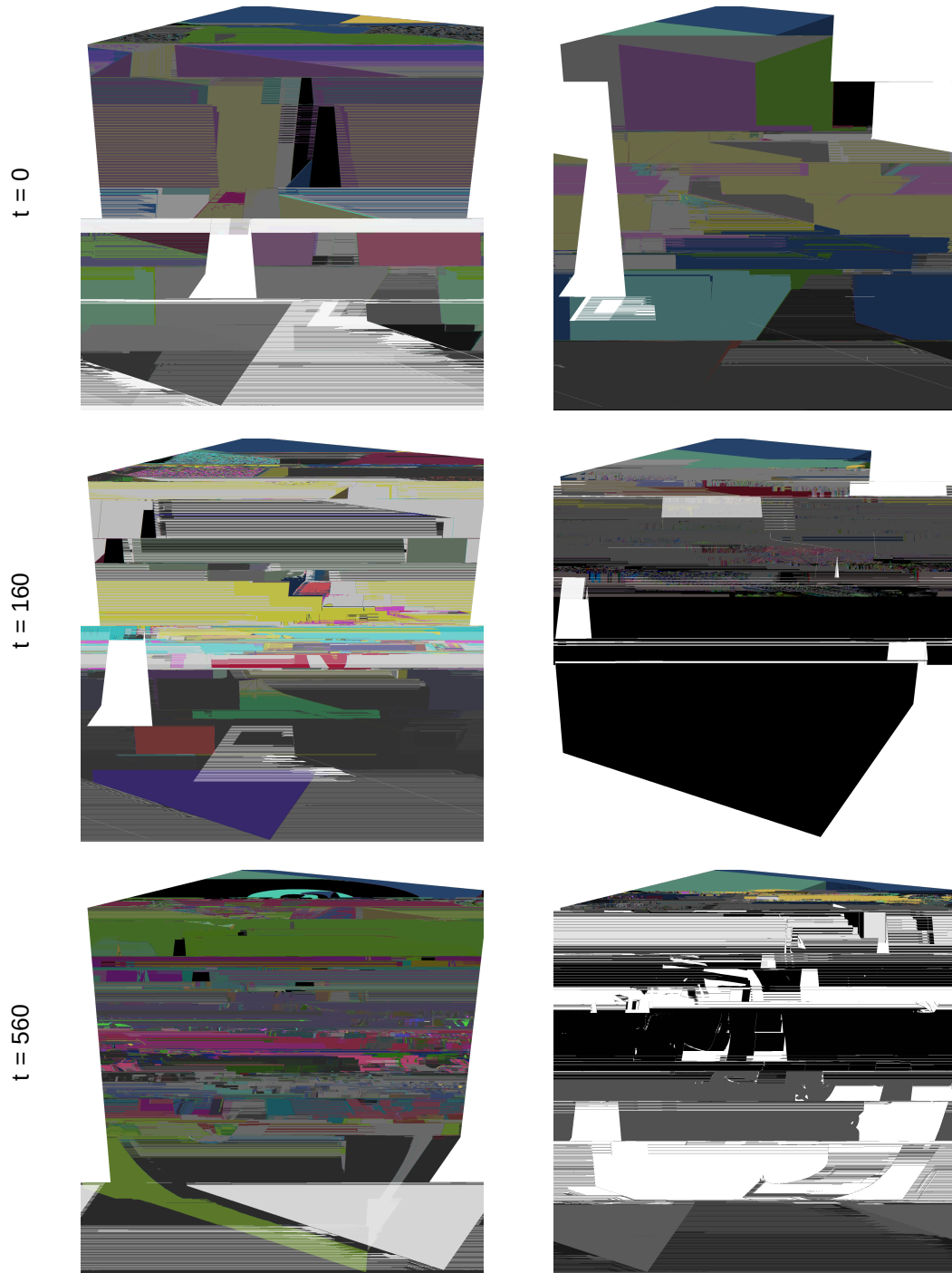


Figure 7. Evolution in three spatial dimensions using the parameters $\beta_2 = 0:1$ and $\beta_3 = 0:6$ (as in Fig. 1), computed on the domain $\Omega = [0; 600]^3$. The figures in the left column show the domains dominated by each species, while those on the right show u_2 and u_3 only in the subdomain $x > 300$.

Proof. Using the definitions of f_h and the discrete Laplacian operator, we can rewrite (4) as

$$(u_{h,t} - \Delta_h u_h - f_h(u_h); v) = 0 \quad \forall v \in V_h;$$

implying that u_h satisfies

$$u_{h,t} - \Delta_h u_h - f_h(u_h) = 0;$$

and therefore, from the definition of the elliptic reconstruction,

$$(u_{h,t}; v) + (\Delta_h u_h; v) + (f_h(u_h); v) = 0 \quad \forall v \in H^1(\Omega); \quad (9)$$

To derive the required bounds, we first decompose the error $e = u - u_h$ into $e := u - R_h u_h$ and $e := R_h u_h - u_h$. Since (5) provides a bound on the reconstruction error, we focus principally on deriving a bound for e . Subtracting (9) from the original weak form (3), we find that

$$(e_t; v) + (\Delta_h e; v) = (f(u) - f_h(u_h); v) \quad \forall v \in H^1(\Omega);$$

and therefore, picking $v = e$, we have

$$\frac{1}{2} \frac{d}{dt} \|e\|_h^2 + \|\Delta_h e\|_h^2 = (f(u) - f_h(u_h); e); \quad (10)$$

To treat the nonlinear term in (10), we use assumption (2) on the growth of f , to find

$$\int_\Omega (f(u) - f_h(u_h)) e \, dx \leq C_f \int_\Omega (1 + |u| + |u_h|) |u - u_h| \, dx;$$

The restriction on f implies that $|f(a) - f(b)| \leq \max_{f \in [1, g]} |f'| (|a| + |b|) \leq 2(|a| + |b|)$, from which, with $a = u$ and $b = u_h$, it follows that

$$\int_\Omega (f(u) - f_h(u_h)) e \, dx \leq 2C_f \int_\Omega |u - u_h| |e| \, dx + \int_\Omega |u - u_h|^{p+1} \, dx; \quad (11)$$

The first term on the right hand side of (11) can be bounded as

$$\int_\Omega |u - u_h| |e| \, dx \leq \int_\Omega |e|^2 + \int_\Omega |e| \, dx \leq \frac{3}{2} \|e\|_h^2 + \frac{1}{2} \|e\|_h^2; \quad (12)$$

For the second term on the right hand side of (11), however, we make use of the bound (7) and (8), yielding

$$\begin{aligned} C_f \int_\Omega |u - u_h|^{p+1} \, dx &\leq C_f \frac{1}{p+2} \int_\Omega |u - u_h|^{p+2} \, dx + \frac{C_f}{p+2} \int_\Omega |e|^{p+2} \, dx \\ &\leq C_f \frac{(1+p)^{p+1}}{p+2} k_L^{p+2}(\Omega) + C_f \frac{1 + (1+p)^{p+1}}{p+2} k_L^{p+2}(\Omega) \\ &= C_1 k_L^{p+2}(\Omega) + C_2 k_L^{p+2}(\Omega); \end{aligned}$$

where

$$C_1 := C_f C \frac{1}{p+2} \quad \text{and} \quad C_2 := C_1 + C_f C \frac{(1+p)^{p+1}}{p+2};$$

Combining this with (12), the error bound (10) becomes

$$\frac{1}{2} \frac{d}{dt} \|e\|_h^2 + \|\Delta_h e\|_h^2 = (f(u) - f_h(u_h); e) \leq 4MC_f \|e\|_h^2 + (1 + 4MC_f) \|e\|_h^2 + C_1 k_L^{p+2}(\Omega) + C_2 k_L^{p+2}(\Omega);$$

Integrating through time, we find that

$$\|e(t)\|_h^2 + \int_0^t \|\Delta_h e\|_h^2 \, dt \leq (1 + 4MC_f) \int_0^t \|e\|_h^2 \, dt + C_2 \int_0^t \|e\|_h^{p+2} \, dt;$$

where we observe that, by construction, $(0) = 0$, and the functional is given by

$$(\cdot)^2 := \int_0^T k_t k^2 + 4MC_f k k^2 + C_1 k k k^2 dt:$$

The inequality $a b \leq a^2 + b^2$ (a consequence of Young's inequality) then implies that

$$\begin{aligned} k(t)k^2 + \int_0^t k k^2 ds &\leq (\cdot)^2 + (1 + 4MC_f) \int_0^t k k^2 ds + C_2 \sup_{s \in [0;t]} k(s) \int_0^t k k^2 ds \\ &\leq (\cdot)^2 + (1 + 4MC_f) \int_0^t k k^2 ds + C_2 \sup_{s \in [0;t]} k(s) k^2 + \int_0^t k k^2 ds : \quad (13) \end{aligned}$$

To bound the final terms on the right hand side using (5), suppose that the maximum size $h_{\max}$ of the mesh used to partition the domain is small enough that for $h < h_{\max}$, the reconstruction error satisfies

$$(\cdot) \leq C_2 4e^{(1+4MC_f)T} \frac{2+}{2};$$

implying that

$$C_2 4 (\cdot)^2 e^{(1+4MC_f)T} \frac{1+}{2} (\cdot)^2:$$

Consider the set

$$I = \{ t \in [0; T] : \sup_{s \in [0; t]} k(s)k^2 + \int_0^t k k^2 ds \leq 4 (\cdot)^2 e^{(1+4MC_f)T} \frac{1+}{2} \}:$$

Upon observing that, by construction, we have $(0) = 0$, this set is clearly not empty since it contains 0 . Moreover, the continuity of $(\cdot)$ in time implies that I must be closed, and thus the maximum of the set is well defined. Thus denoting $t^* = \max I$, we suppose that $t^* < T$. Then, for $t = t^*$:

$$C_2 \sup_{s \in [0;t]} k(s)k^2 + \int_0^t k k^2 ds \leq 4 (\cdot)^2 e^{(1+4MC_f)T} \frac{1+}{2} (\cdot)^2:$$

Substituting this into (13) we find that, for $t = t^*$

$$k(t)k^2 + \int_0^t k k^2 ds \leq 2 (\cdot)^2 + (1 + 4MC_f) \int_0^t k k^2 ds;$$

from which Gronwall's inequality implies

$$k(t)k^2 + \int_0^t k k^2 ds \leq 2 (\cdot)^2 e^{(1+4MC_f)T}:$$

Since this is true for all t (and the integral on the left is non-decreasing), it follows that

$$\sup_{s \in [0;t]} k(s)k^2 + \int_0^t k k^2 ds \leq 2 (\cdot)^2 e^{(1+4MC_f)T};$$

which contradicts the assumption that $t^* < T$ due to the continuity of $(\cdot)$ in time.

Consequently, we have

$$k(t)k^2 + \int_0^t k k^2 ds \leq 2e^{(1+4MC_f)T} \int_0^t k_t k^2 + 4MC_f k k^2 + C_1 k k k^2 ds;$$

for any $s \in [0; T]$. Applying the triangle inequality and invoking the bound (5) for $(\cdot)$ then produces the required bounds.

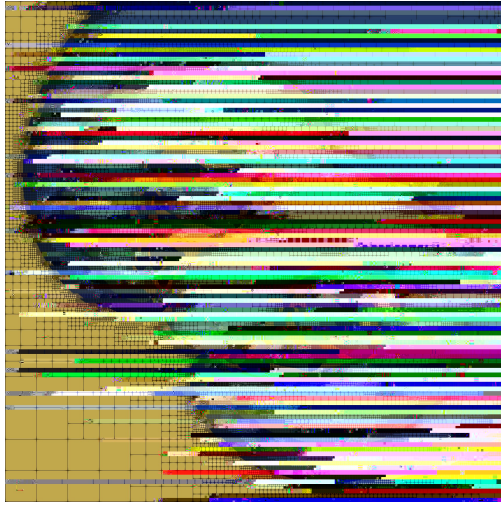
We note that the above error bounds are computable. Indeed, assuming the existence of the constant M bounding the L^1 -norm of the finite element solution u_h is not unreasonable since we can assume to have computed it, and thus have access to its maximal and minimal values. Hence both bounds of Theorem 5.1 are computable since they depend only on the discrete solution and problem data.

The error indicator which we use to mark mesh elements for either refinement or coarsening is derived from the a posteriori error bound of Theorem 5.1 and is of the form

$$E_1(u^n)^2 + E_0 \frac{u^n - u^{n-1}}{\tau_n}^2;$$

which may naturally be broken into contributions from each element by observing the structure of E_r in (6). We remark that a posteriori bounds for the time discretisation by the Crank-Nicolson method are also available [4, 8]. Given the nature of the simulations, however, whereby the length-scales present do not change over time, (but only in position,) the incorporation of a full-space time a posteriori analysis in the spirit of [8] was not deemed necessary in this case. Crucially, however, the modified Crank-Nicolson method of [8] was used in the present context of temporal mesh-modification.

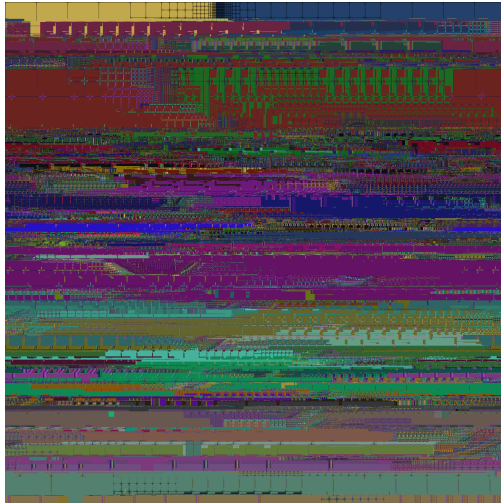
Figure 8 shows some examples of the computational meshes used to obtain the results of Section 4, reporting the number of elements saved compared to an equivalent uniform mesh in each case (which may be used as a rough estimate of the computational effort required to compute the solution). What this clearly demonstrates is the effectiveness of the resulting adaptive scheme, since the number of elements required is reduced by over 50% in each case and typically dramatically more. Moreover, examining the areas in which the algorithm has opted to refine or coarsen the mesh indicates that computational effort (in the form of high mesh resolution) is



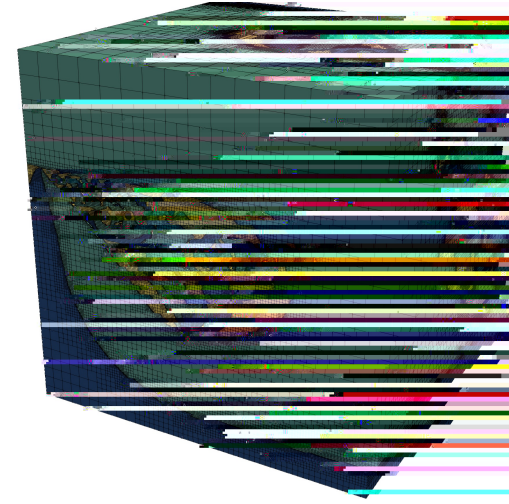
(a) Adapted mesh for the solution shown in Fig. 2d containing 18,418 elements (73% saving over equivalent uniform mesh)



(b) Adapted mesh for the solution shown in Fig. 3d, containing 8,935 elements (83% saving over equivalent uniform mesh)



(c) Adapted mesh for the solution shown in Fig. 6d, containing 5,953 elements (91% saving over equivalent uniform mesh)



(d) Adapted mesh for the solution shown in Fig. 7, containing 1,015,660 elements (51% saving over equivalent uniform mesh)

Figure 8. Some examples of meshes produced by the adaptive algorithm, demonstrating the reduction in the number of elements required compared to a uniform mesh with the same resolution around the layers.

their work Contento and co-authors [14] hypothesised the existence of droplet-like structures in a spreading wedge which is close to that shown in Fig. 1, although they did not find a practical realisation of such a pattern and assumed that it would be unstable [14]. Here we found a stable pattern consisting of droplets in a spreading wedge. It is worth observing, however, that in

the spread is based on pairwise interactions between species and, unlike in the cited work, the corresponding 1D case does not allow the spread of a travelling pulse involving all three species. Moreover, the authors of [14] hypothesised that their pattern would exist under conditional cyclic competition, while the droplet-shaped structures in Fig. 1 are found in classical (i.e. unconditional) cyclic competition. It therefore still remains to be determined whether the patterns predicted by Contento and co-authors are actually possible in the case of conditional cyclic competition involving local bistability.

The pattern of spread shown in Fig. 4 is of particular interest, not only because of the apparent regularity in the direction of movement and irregularity in the opposite direction. A novel feature of the pattern seems to be the coexistence of two different waves moving towards the left hand boundary: one wave is a wave of regularity composed of almost parallel bands in the middle and two wedge-shaped waves of chaos on each side of the bands. Our simulations show a long term coexistence of both types of waves. Using this pattern one can describe a complex spread of species involving regular and irregular population patches.

These newly demonstrated patterns of travelling waves with spatially regular structure can be interpreted in terms of the definition of convective stability introduced by [42]. Indeed, the developing regular travelling structures are convectively stable since they emerge as a result of complex spatio-temporal interactions. However, they are not globally stable, as shown in Fig. 4: depending on the initial conditions, both the waves of regularity and the waves of chaos can be simultaneously realised in the same system.

The spatially regular geometric shapes found by this study to exist in the wake of spreading waves may have applications in the life sciences. It is well known that the distribution of vegetation in semiarid or other regions show regular band-shaped patterns which slowly move over time [2, 26, 40]. The common point of view on the origin of these vegetation patterns is the interaction between the soil and plants controlled by the level of moisture via various mechanisms such as Turing pattern formation or periodic travelling waves [24, 17]. Here we suggest an alternative mechanism for the formation such bands, due to the interaction of competitive plant species which, for instance, does not require the existence of a steady gradient in the system.

The pattern containing regular droplet-shaped structures shown in Fig. 1 and Fig. 3 can potentially be realised on growing domains [6, 36] such as in the pigmentation and relief-like patterns found on mollusc shells, which remain a long standing question [9, 19]. Previously, it was suggested that regular patterns in mollusc shells are the result of inhibitor-activator type interactions via a Turing mechanism. Here we show that similar patterns can be produced by a cyclic competition type of interaction via a non-Turing mechanism. Finally, the transient glider-type patterns shown in Fig. 6 in the case of conditional cyclic competition provide an example of a new mechanism of patchy spread of invasive species. This new pattern can be used to improve our understanding and modelling of biological invasions since empirical observations often report that the spread of a species into the habitat occupied by another species occurs via the propagation of irregular patches [43]. This also supports the recent ecological theory of invasional meltdown, when an invasive species facilitates the invasion of some other invasive species [35]. Note that unlike the original concept of invasional meltdown, suggesting mutual facilitation of invasion of species via mutualistic interactions, in our case we consider the case of antagonistic competitors [44].

Our results have also allowed us to improve our understanding of the role of dimensionality on the pattern formation in the considered type of models. This can be seen by comparing Fig. 1 and Fig. 6 alongside the corresponding 1D simulations (not shown here for the sake of simplicity). In one spatial dimension, a wave of mutual spread of three species is impossible for the given parameters: only pairwise switch waves are observed. With two spatial dimensions, the droplet-shape pattern can emerge even though it is simply the result of the pairwise interaction of plane

waves, as shown in Fig. 5 (the round-shaped interface can be formally considered as a plain wave in polar coordinates). Thus, increasing from one to two spatial dimensions allows for species coexistence through a structure which was previously impossible. Interestingly, adding a third dimension continues to allow the persistence of the droplet-shape structure, although we argue here that the pattern remains primarily two-dimensional since the three dimensional droplets are observed to have a prismatic structure, and can still be described via pairwise interactions of locally plain prismatic waves.

Bearing in mind the large domains and long time scales required for the full solution dynamics to evolve, it is clear that the computational cost of these simulations would be prohibitively expensive using a uniform mesh, an issue which is amplified in three spatial dimensions. Instead, the adaptive numerical method described in Section 3, based on the novel computable error indicator derived in Section 5, allows us to obtain accurate simulations using just a fraction of the computational effort of an equivalent non-adaptive scheme, as demonstrated by the adapted computational meshes shown in Fig. 8. The savings this method provides means that highly accurate simulations of this model are within reach of researchers without needing access to high performance computing facilities. Moreover, since the error analysis of Section 5 is applicable to a much wider class of semilinear reaction-diffusion problems, the adaptive method which we describe can be easily applied by researchers wishing to study other phenomena.

We should point out that our numerical investigation of the model cyclic Lotka-Volterra system is by no means exhaustive. We do not claim that combined with the previous studies of the system [31, 34, 2, 12, 14] we have now completed a full classification of possible patterns. Further research will be needed specially to further explore the case of conditional cyclic competition. Another interesting direction is to further explore the influence of the number of spatial dimensions on the species persistence. In other words, it is interesting to verify whether or not adding a third dimension will enhance the coexistence of all species and which possible patterns of mutual coexistence can occur. This is a biologically relevant question which is important for understanding, for example, the coexistence of competing bacterial strains or microalgae in laboratory and natural conditions.

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