Non-reciprocal interactions promote diversity

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We study a process of pattern formation for a model of species anchored to the nodes of a network, where local reactions take place, and that experience non-reciprocal long-range interactions. We show that the system exhibits a stable homogeneous equilibrium whenever only local interactions are considered; we prove that such equilibrium can turn unstable once suitable non-reciprocal long-range interactions are allowed for. The instability, precursor of the emerging spatio-temporal patterns, can be traced back, via a linear stability analysis, to the complex spectrum of an interaction non-symmetric Laplace operator. Taken together, our results pave the way for the understanding of the diversity of behaviours found in many ecological, chemical and physical systems composed by interacting parts, once no diffusion takes place.

We live in an interconnected world \cite{1,2} where complex patterns \cite{3} spontaneously emerge from the intricate web of nonlinear interactions existing between the basic units by which the system under study is made of \cite{4}. These emergent structures can be found in the synchronised activity of neurones, resulting from the exchange of electrochemical signals via synapses \cite{5,6}, as well as in the geometric visual hallucinations product of the retinocortical map linking the retina and the striate cortex \cite{7,8}. Such self-organised structures can also manifest in groups of fireflies that flash at unison, each one observing the behaviour of their close neighbours \cite{9}. Or they can materialise as the striped or spotted motifs on the skin of the zebrafish \textit{Danio rerio}, due to the long-range interactions between melanophores and xantophores, without requiring diffusion nor any kind of cell motion \cite{10,11}.

The latter phenomena, as well as many other ones modelled within a similar framework of local reactions and long-range interactions without displacement, cannot be ascribed to a Turing instability \cite{12}, a paradigm for pattern formation. Indeed the latter requires a diffusive process, whereas the common key factor linking the above examples is the immobility of the reacting species and the existence of a web of long-range interactions due to some signal propagation.

In this work we set the theoretical basis for the understanding of self-organisation in diffusionless systems where asymmetric long-range interactions play a pivotal role. Network science \cite{11,12} provides a natural framework where to study such phenomena. Indeed local interactions can be described by a dynamical system evolving on each node, while long-range interactions can be modelled by links connecting the nodes of the network, allowing thus the latter to “communicate”. In the aforementioned examples, the system converges to an homogeneous solution, being stationary or time varying, once only local interactions are taken into account, while heterogeneous solutions spontaneously emerge in presence of a suitable web of interactions among the units.

A preliminary result in this direction has been recently proposed in \cite{13} with the assumption of reciprocal non-local interactions and treating the latter in a mean-field setting. Authors have been able to prove that the stable homogeneous solution existing once the long-range interactions have been silenced, can turn unstable by introducing a suitable non-local coupling and eventually lead to the emergence of a spatially (and temporally) dependent solution. The aim of the present work is to make one step forward by studying the general case of non-reciprocal interactions. Indeed, the interactions existing among the constituting units are often not symmetric; this is the case of plant-animal mutualistic networks \cite{14,15} or the case of olfactory receptor neurones in the Drosophila antenna \cite{16}, just to mention a few.

Anticipating our conclusion, we can claim that the diversity observed in Nature, being associated to spatial or temporal heterogeneity, is promoted by non-reciprocal long-range interactions. The onset of the instability, precursor of the pattern, can be detected with a linear stability analysis, providing a condition on the complex spectrum of a non-symmetric consensus Laplacian operator. The proposed framework is general enough to cover systems displaying a fixed-point or a limit cycle homogeneous solution, once we silence the long-range interactions. In conclusion, the proposed mechanism provides the way for alternative routes to pattern formation, beyond the Turing one \cite{12,17}, suitable for all phenomena where diffusion is not the main driver of heterogeneity, i.e., diversity, and thus opening new possibilities for modelling ecological, chemical and physical interacting systems, endowed with non-reciprocal couplings.

More specifically, we consider a dynamical system composed by \(n\) identical parts and we assume the \(d\)-dimensional vector, \(x^{(i)}(t) = (x^{(i)}_{1}(t),\ldots,x^{(i)}_{d}(t))^\top\), representing the state of the \(i\)-th copy. The isolated systems are described by a mean-field hypothesis

\[
\frac{dx^{(i)}}{dt} = f(x^{(i)}) \quad \forall i = 1,\ldots,n, \tag{1}
\]

where \(f\) is a generic nonlinear function responsible for
the local interactions. Let us now allow each system to possess nonlocal interactions, i.e., its behaviour now depends on the state of other units of the system; moreover we assume the latter to be described by
\[
\frac{d\mathbf{x}^{(i)}}{dt} = \frac{1}{k^{(in)}_i} \sum_j A_{ij} \mathbf{F}(\mathbf{x}^{(i)}, \mathbf{x}^{(j)}) \quad \forall i = 1, \ldots, n, \quad (2)
\]
where \(A_{ij}\) is the (possibly weighted) non-symmetric adjacency matrix encoding the long-range interactions, i.e., \(A_{ij} = 1\) if and only if node \(j\) influences node \(i\). Let \(k^{(in)}_i = \sum_j A_{ij}\) be the in-degree of node \(i\) and observe that we allow \(A_{ii} = 1\), thus the in-degree takes into account also the possible self-loops. Finally, \(\mathbf{F}(\mathbf{x}^{(i)}(t), \mathbf{x}^{(j)}(t))\) is a nonlinear function that describes the effect of the \(j\)-th system on the \(i\)-th one; moreover we require that \(\mathbf{F}(\mathbf{x}^{(i)}, \mathbf{x}^{(j)}) = \mathbf{f}(\mathbf{x}^{(i)})\), namely the self-interaction is represented by the original nonlinear function \(\mathbf{f}\) describing the evolution of the isolated systems \([31]\). Let us observe that the right hand side of (2) can be rewritten as the average of the interactions perceived by node \(i\),
\[
\langle \mathbf{F}(\mathbf{x}^{(i)}, \mathbf{y}^{(j)}) \rangle = \sum_j A_{ij} \mathbf{F}(\mathbf{x}^{(i)}, \mathbf{x}^{(j)}) / k^{(in)}_i,
\]
hence describing the mean-field ansatz.

By defining the matrix
\[
\mathcal{L}_{ij} = \frac{A_{ij}}{k^{(in)}_i} - \delta_{ij}, \quad (3)
\]
we can rewrite Eq. (2) as
\[
\frac{d\mathbf{x}^{(i)}}{dt} = \mathbf{f}(\mathbf{x}^{(i)}) + \sum_j \mathcal{L}_{ij} \mathbf{F}(\mathbf{x}^{(i)}, \mathbf{x}^{(j)}) \quad \forall i = 1, \ldots, n. \quad (4)
\]
Once the long-range interactions are silenced and each node interacts only with itself, i.e., \(\mathbf{A} = \mathbf{I}_n\), being the \(n \times n\) identity matrix, then \(\mathcal{L} = 0\) and thus Eq. (4) reduces to (1), i.e., the \(n\) isolated systems. Let us observe that in the case of reciprocal interactions, the above defined matrix \(\mathcal{L}\) corresponds to the consensus Laplace operator \([18, 21]\), also named reactive Laplace in \([13]\), whose spectrum is real and non-positive. In the case under scrutiny, involving non-reciprocal interactions, the spectrum is generally complex but one can prove that \(\lambda_1 = 0\) is still an eigenvalue associated to the uniform eigenvector \(\phi^{(1)} \sim (1, \ldots, 1)^T\). Moreover the Gershgorin circle theorem \([22]\) allows to prove that the real part of the spectrum of \(\mathcal{L}\) is contained in the strip \([-2, 0]\) in the complex plane, hence \(\mathcal{L}\) is stable having all the eigenvalues but 0 with a negative real part.

Let us assume \(\mathbf{x}^{(i)}(t) = \mathbf{s}(t), \; i = 1, \ldots, n\), to be a solution of the initial system (1); then because of the above assumption on \(\mathbf{F}\) and of the definition of \(k^{(in)}_i\), it is also a spatially independent solution of Eq. (4). To study the bifurcation of patchy solutions from the stable homogeneous one, \(\mathbf{s}(t)\), we consider a node dependent perturbation about the latter, \(\mathbf{u}^{(i)}(t) = \mathbf{x}^{(i)}(t) - \mathbf{s}(t)\), whose evolution can be studied by inserting it into Eq. (1) and then keeping only first order terms, assumed to be small enough, hence for all \(i = 1, \ldots, n\)
\[
\frac{d\mathbf{u}^{(i)}}{dt} = [\mathbf{J}_1(\mathbf{s}(t)) + \mathbf{J}_2(\mathbf{s}(t))] \mathbf{u}^{(i)} + \sum_j \mathcal{L}_{ij} \mathbf{J}_2(\mathbf{s}(t)) \mathbf{u}^{(j)}, \quad (5)
\]
where we have introduced the Jacobian matrices \(\mathbf{J}_1 = \partial_x \mathbf{F}(\mathbf{s}, \mathbf{s})\), i.e., the derivatives are computed with respect to the first group of variables, and \(\mathbf{J}_2 = \partial_{\mathbf{x}_2} \mathbf{F}(\mathbf{s}, \mathbf{s})\), i.e., the derivatives are performed with respect to the second group of variables. In both cases the derivatives are evaluated on the reference solution \(\mathbf{s}\).

This latter equation encodes \(n\) linear systems involving matrices with size \(d \times d\). To progress with the analytical understanding, we assume the existence of an orthonormal eigenbasis for \(\mathcal{L}\) and then we project the former equation onto each eigendirection, i.e., \(\mathbf{u}^{(i)} = \sum_\alpha \mathbf{u}^{(\alpha)} \phi^{(\alpha)}_i\), to eventually obtain (see Supplementary Material)
\[
\frac{d\mathbf{u}^{(\alpha)}}{dt} = \left[\mathbf{J}(\mathbf{s}(t)) + \mathbf{J}_2(\mathbf{s}(t)) \Lambda^{(\alpha)}\right] \mathbf{u}^{(\alpha)} \quad \forall \alpha = 1, \ldots, n, \quad (6)
\]
where \(\mathbf{J} = \mathbf{J}_1 + \mathbf{J}_2\) and \(\Lambda^{(\alpha)}\) is the eigenvalue relative to the eigenvector \(\phi^{(\alpha)}\). The above equation enables us to infer the (in)stability of the homogeneous solution, \(\mathbf{s}(t)\), by studying the Master Stability Function \([23, 24]\), namely the largest Lyapunov exponent of Eq. (6).

To make one step further in the study of the problem, let us hypothesise that each isolated system converges to the same stationary point, i.e., the stable homogeneous solution is stationary, \(\mathbf{s}(t) = \mathbf{s}_0\). Hence Eq. (6) rewrites for all \(\alpha = 1, \ldots, n\), as
\[
\frac{d\mathbf{u}^{(\alpha)}}{dt} = \left[\mathbf{J}(\mathbf{s}_0) + \mathbf{J}_2(\mathbf{s}_0) \Lambda^{(\alpha)}\right] \mathbf{u}^{(\alpha)} := \mathbf{J}^{(\alpha)} \mathbf{u}^{(\alpha)}. \quad (7)
\]
The homogeneous solution will prove unstable to spatially dependent perturbations if (at least) one eigenmode \(\hat{\alpha}\) exists for which the largest real part of the eigenvalues, \(\Lambda_1\), of \(\mathbf{J}^{(\hat{\alpha})}\) is positive, the latter being known in the literature with the name of dispersion relation, hereby denoted by \(\rho_0 = \max_{i=1,\ldots,d} \Re \Lambda_i(\Lambda^{(\hat{\alpha})})\), where we emphasised the dependence on the spectrum of the Laplace matrix.

For sake of simplicity, let us assume the local systems to be 2 dimensional, i.e., \(d = 2\) in Eq. (1). Then, being the eigenvalues of \(\mathbf{J}^{(\alpha)}\) the solutions of the second order equation
\[
\lambda^2 - \tr(\mathbf{J}^{(\alpha)}) \lambda + \det(\mathbf{J}^{(\alpha)}) = 0,
\]
we can adapt to the present case the analysis done in \([25, 26]\) and express the condition for the onset of instability, i.e., \(\rho_0 > 0\), as follows
\[
\exists \hat{\alpha} > 1 \text{ s.t. } S_2 \left(\Re \Lambda^{(\hat{\alpha})}\right) \left(\Im \Lambda^{(\hat{\alpha})}\right)^2 \leq -S_1 \left(\Re \Lambda^{(\hat{\alpha})}\right), \quad (8)
\]
where \( S_2(\xi) \), resp. \( S_1(\xi) \), is a second, resp. fourth, degree polynomial in \( \xi \) (see Supplementary Material for more details).

To illustrate the potential of the theory let us consider a specific application dealing with a Volterra model \(^{27}\) that describes the interactions of prey and predators in an ecological setting:

\[
\begin{align*}
\frac{dx}{dt} &= -dx + c_1 xy \\
\frac{dy}{dt} &= ry - sy^2 - c_2 xy .
\end{align*}
\]

(9)

Here \( x \) denotes the concentration of predators, while \( y \) stands for the preys, and all the parameters are assumed to be positive. The Volterra model \((9)\) admits a nontrivial fixed-point, \( x^* = \frac{c_1 r - sd}{c_2 r^2}, \ y^* = \frac{d}{c_1} \), which is positive and stable, provided that \( c_1 r - sd > 0 \).

Following the above presented scheme, let us now consider \( n \) replicas of the model \((9)\), each associated to a different ecological niche and indexed by the node index \( i \). Assume also that, besides local interactions, species in a given niche can sense the long-range interactions with other communities of prey or predator, populating neighboring nodes. For instance, predators can benefit from a coordinated action to hunt in a whole neighbourhood, e.g., predators can push preys and signal their presence with sounds. And, more importantly, such interactions are not necessarily reciprocal. For sake of definitiveness we will study the coupling defined by:

\[
\begin{align*}
\frac{dx_i}{dt} &= -dx_i + ac_1yi \sum_j \frac{A_{ij}}{\xi^{|\xi_i-j|}} x_j + (1 - a)c_1 x_i \sum_j \frac{A_{ij}}{\xi^{|\xi_i-j|}} y_j \\
\frac{dy_i}{dt} &= ry_i - sy_i^2 - c_2 x_i \sum_j \frac{A_{ij}}{\xi^{|\xi_i-j|}} x_j ,
\end{align*}
\]

(10)

where the matrix \( A_{ij} \) encodes for the asymmetric interactions among animals in patches \( i \) and \( j \). The parameter \( a \in [0, 1] \) describes the relative strength with which the predators replication rate in node \( i \) increases because of the “in-node” predation or because of the interactions among predators in the neighbours. The case \( a = 1 \) corresponds to a purely in-node process while if \( a = 0 \) predators act only in the nearby patches. Preys feel the competition for the resources with other preys of the same niche; moreover they experience the local action of predators, i.e., in the same niche, as well as the presence of far away predators that can signal their presence, e.g., with sounds. Birth and death of both species are local, i.e., due to resources available in-node. The latter equation is the analogous of Eq. \((2)\) for the Volterra model and it can be straightforwardly rewritten as follows by introducing the Laplace matrix \( L \)

\[
\begin{align*}
\frac{dx_i}{dt} &= -dx_i + c_1 x_i y_i + ac_1 y_i \sum_j L_{ij} x_j + \\
&\quad + (1 - a)c_1 x_i \sum_j L_{ij} y_j \\
\frac{dy_i}{dt} &= ry_i - sy_i^2 - c_2 x_i \sum_j L_{ij} x_j ,
\end{align*}
\]

(11)

where we can now recognise the \( n \) copies of the isolated Volterra system \((2)\) (left most term in the right hand side) and the coupling due to the long-range interactions.

We can thus compute the explicit form of the polynomials \( S_1(\xi) \) and \( S_2(\xi) \) as a function of the model parameters (see Supplementary Material) and characterise the instability region defined by \((8)\) as reported in Fig. \(1\) where we show in the complex plane \((\Re \Lambda, \Im \Lambda)\) the regions for which the instability condition is satisfied (grey), for a given set of parameters. Patterns do emerge if there exists at least on eigenvalue \( \Lambda^{(a)} \) belonging to this region. For sake of simplicity, we hereby assume the non-reciprocal interactions to be described by a directed Erdős-Rényi network made of 50 nodes and the probability to create a directed link to be 0.5. The symmetric coupling is obtained by considering all the existing links to be reciprocal ones. Let us stress that, in this case, even if the consensus Laplace is not symmetric, the eigenvectors are real and non-positive (see Supplementary Material ). In conclusion, if the model parameters shape an instability region that doesn’t intersect the real axis and thus only non-reciprocal coupling can exhibit complex eigenvalues (white dots) entering into the instability region and thus initiate the pattern as shown in panel b) where we report \( y_i(t) \) vs \( t \) starting from initial conditions close to the stable equilibrium. Any symmetric coupling determines real eigenvalue (black dots in panel a)) that cannot give rise to the instability (data not shown). The underlying coupling is a directed Erdős-Rényi network with \( n = 50 \) nodes and a probability for a direct link to exist between two nodes is \( p = 0.5 \).

![FIG. 1: Instability region and patterns for the Volterra model. In panel a) we report the region of the complex plane (\( \Re \Lambda, \Im \Lambda \)) for which the instability condition is satisfied (grey). For the chosen parameters values (\( c_1 = 2, c_2 = 13, r = 1, s = 1, d = 0.4 \) and \( a = 0.05 \)) we can observe that the instability region doesn’t intersect the real axis and thus only non-reciprocal coupling can exhibit complex eigenvalues (white dots) entering into the instability region and thus initiate the pattern as shown in panel b) where we report \( y_i(t) \) vs \( t \) starting from initial conditions close to the stable equilibrium. Any symmetric coupling determines real eigenvalue (black dots in panel a)) that cannot give rise to the instability (data not shown). The underlying coupling is a directed Erdős-Rényi network made of 50 nodes and the probability to create a directed link to be 0.5. The symmetric coupling is obtained by considering all the existing links to be reciprocal ones. Let us stress that, in this case, even if the consensus Laplace is not symmetric, the eigenvectors are real and non-positive (see Supplementary Material ). In conclusion, if the model parameters shape an instability region that doesn’t intersect the real axis (see panel a) in Fig. \(1\), then only an asymmetric coupling can drive the instability and the ensuing patterns (see panel b) in Fig. \(1\), while this is impossible for a web of reciprocal long-range interactions. On the other hand, once the instability region intersects the real axis (see Fig. \(3\) in Supplementary Material ), then also a symmetric coupling can trigger the instability. As anticipated, the proposed method goes beyond the framework presented above dealing with stationary homogeneous solution, but can be extended to study systems exhibiting an oscillating behaviour, being the latter a regular or a chaotic one. To support this claim, let us study for sake of definitiveness the Stuart-Landau system.
system admits an homogeneous stable limit cycle solution and thus the driver for the diversity of patterns are the key factor in the disruption of the homogeneous system, described by non-reciprocal interactions, temporal patterns. The intrinsic asymmetries within conditions for the instability and the ensuing spatial or
modelled with a mean-field scheme, return a consensus of diffusion. Long-range non-reciprocal interactions, self-organisation can manifest without the presence of non-reciprocal long-range interactions, to show that existence of non-reciprocal couplings able to trigger the instability by destabilising the limit cycle solution, even-ultually driving the system toward a new heterogeneous state. Assume again the long-range interactions to be modelled through a mean field ansatz \cite{2}

\[
\frac{dw_j}{dt} = \frac{\sigma}{k_j^{(m)}} \sum_{\ell} A_{j\ell} w_\ell - \beta w_j |w_j|^2 \\
= \sigma w_j - \beta w_j |w_j|^2 + \sigma \sum_{\ell} \mathcal{L}_{j\ell} w_\ell ,
\]

where \( w_j \) is the complex state variable of the \( j \)-th SL system and \( A_{j\ell} \) encodes the non-reciprocal coupling. Such system admits an homogeneous stable limit cycle solution if \( \sigma_R > 0 \) and \( \beta_R > 0 \). We can then show the existence of non-reciprocal couplings able to trigger the instability by destabilising the limit cycle solution, eventually driving the system toward a new heterogeneous wavy solution. Indeed, according to the theory hereby developed, we can always determine model parameters allowing for an instability region in the complex plane (see Supplementary Material ), that does not intersect the real axis; the spectrum of a reciprocal web of long-range interactions could thus never belong to the instability region (black dots in Fig. 2) and any perturbation fades away. On the other hand, the complex spectrum associated to non-reciprocal couplings could intersect the instability region (white dots in Fig. 2), driving thus the system toward the formation of patterns.

In conclusion, we have proposed and analysed a mechanism for pattern formation, being the latter stationary or time dependent, rooted on the presence of non-reciprocal long-range interactions, to show that self-organisation can manifest without the presence of diffusion. Long-range non-reciprocal interactions, modelled with a mean-field scheme, return a consensus Laplace operator, whose complex spectrum sets the conditions for the instability and the ensuing spatial or temporal patterns. The intrinsic asymmetries within the system, described by non-reciprocal interactions, are the key factor in the disruption of the homogeneous solution and thus the driver for the diversity of patterns one can observe in Nature. The proposed mechanism complements thus the Turing one \cite{12, 17} and it is suitable for all phenomena where pattern emergence is not driven by a diffusive process but immobile species interact through non-reciprocal long-range couplings.

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Let us consider the homogeneous solution $s(t)$ and a spatially dependent perturbation about the latter, $x^{(i)}(t) = s(t) + u^{(i)}(t)$, then by inserting this information into Eq. (3) (main text) and by retaining only the linear terms in $u^{(i)}$ we obtain

$$\frac{du^{(i)}}{dt} = \frac{dx^{(i)}}{dt} - \frac{ds}{dt} = \frac{1}{k^{(m)}_i} \sum_j A_{ij} F(s + u^{(i)}, s + u^{(j)}) - f(s)$$

$$= \frac{1}{k^{(m)}_i} \sum_j A_{ij} \left( \sum_{\ell} \partial_{x^{(i)}_\ell} F(s, s) u^{(i)}_{\ell} + \sum_{\ell} \partial_{x^{(j)}_\ell} F(s, s) u^{(j)}_{\ell} \right)$$

$$= \sum_{\ell} \partial_{x^{(i)}_\ell} F(s, s) u^{(i)}_{\ell} + \frac{1}{k^{(m)}_i} \sum_j A_{ij} \sum_{\ell} \partial_{x^{(j)}_\ell} F(s, s) u^{(j)}_{\ell}$$

$$= J_1 u^{(i)} + \frac{1}{k^{(m)}_i} \sum_j A_{ij} J_2 u^{(j)} \quad \forall i = 1, \ldots, n,$$

where we recall that $J_1 = \partial_x F(s, s)$ and $J_2 = \partial_{x^2} F(s, s)$. By observing that $f(x) = F(x, x)$ one can prove that $\partial_x f := J = J_1 + J_2$. Hence by slightly rewriting the previous equation, we obtain

$$\frac{du^{(i)}}{dt}(t) = J_1 u^{(i)} + \frac{1}{k^{(m)}_i} \sum_j A_{ij} J_2 u^{(j)} = J_1 u^{(i)} + J_2 u^{(i)} + \sum_j \left( \frac{A_{ij}}{k^{(m)}_i} - \delta_{ij} \right) J_2 u^{(j)}$$

$$= (J_1 + J_2) u^{(i)} + \sum_j \mathcal{L}_{ij} J_2 u^{(j)}$$

$$= J u^{(i)} + \sum_j \mathcal{L}_{ij} J_2 u^{(j)}, \quad \forall i = 1, \ldots, n,$$  \hspace{1cm} (13)

where we used the matrix $\mathcal{L}$, given by Eq. (3) (main text).
By introducing the \( n \times d \) vector \( \mathbf{u} = ((\mathbf{u}^{(1)})^\top, \ldots, (\mathbf{u}^{(n)})^\top)^\top \), we can eventually rewrite the latter equation in a compact form as:

\[
\frac{d\mathbf{u}(t)}{dt} = [(\mathbf{J}_1 + \mathbf{J}_2) \otimes \mathbf{I}_n + \mathbf{J}_2 \otimes \mathcal{L}] \mathbf{u} = [\mathbf{J} \otimes \mathbf{I}_n + \mathbf{J}_2 \otimes \mathcal{L}] \mathbf{u},
\]

where \( \otimes \) denotes the Kronecker product of matrices. In this way we emphasise the role of the Jacobian of the isolated system and the one for the coupling part, that vanishes once we assume \( \mathbf{A} = \mathbf{I}_n \).

The Eq. (13) is a linear system involving matrices with size \( nd \times nd \). One can reduce the complexity of the latter by assuming the existence of an orthonormal eigenbasis of \( \mathcal{L} \), \( \phi^{(\alpha)} \), \( \alpha = 1, \ldots, n \), with associated eigenvalue \( \Lambda^{(\alpha)} \leq 0 \). Then by rewriting \( \mathbf{u}^{(i)} = \sum_\beta \mathbf{u}^{(\beta)} \phi_i^{(\beta)} \) and inserting the latter into (13) we obtain

\[
\sum_\beta \frac{d\mathbf{u}^{(\beta)}(t)}{dt} \phi_i^{(\beta)} = \sum_\beta \mathbf{J}(s(t))\mathbf{u}^{(\beta)}(s(t)) \phi_i^{(\beta)} + \sum_\beta \sum_j \mathcal{L}_{ij} \mathbf{J}_2(s(t))\mathbf{u}^{(\beta)}(s(t)) \phi_j^{(\beta)}
\]

\[
= \sum_\beta \mathbf{J}(s(t))\mathbf{u}^{(\beta)}(s(t)) \phi_i^{(\beta)} + \sum_\beta \Lambda^{(\beta)} \mathbf{J}_2(s(t))\mathbf{u}^{(\beta)}(s(t)) \phi_i^{(\beta)}.
\]

Observing that \( \sum_i \phi_i^{(\alpha)} \phi_i^{(\beta)} = \delta_{\alpha\beta} \), we can multiply the previous equation by \( \phi_i^{(\alpha)} \) and by summing over \( i \) we can obtain Eq. (8) (main text), namely

\[
\frac{d\mathbf{u}^{(\alpha)}(t)}{dt} = \mathbf{J}(s(t))\mathbf{u}^{(\alpha)} + \Lambda^{(\alpha)} \mathbf{J}_2(s(t))\mathbf{u}^{(\alpha)} \quad \forall \alpha = 1, \ldots, n.
\]

Assuming to deal with \( d = 2 \) dimensional systems, one can realise that the eigenvalues of \( \mathbf{J}^{(\alpha)} \), \( \lambda_i \), are the solutions of the second order equation.

\[
\lambda_i^2 - \text{tr}\mathbf{J}^{(\alpha)} \lambda_i + \det\mathbf{J}^{(\alpha)} = 0 \quad \forall i = 1, \ldots, n.
\]

Note that if on the other hand, we were interested in studying \( d > 2 \) dynamical systems, then we should consider roots of \( d \)-degree polynomial equations for which there is no general closed form solution and thus one has to recur to numerics to determine the instability region.

One can express the real part of the above roots as:

\[
\Re \lambda_i = \frac{1}{2} \left( \text{Re}\text{tr}\mathbf{J}^{(\alpha)} + \gamma \right),
\]

where

\[
\gamma = \sqrt{A + \sqrt{A^2 + B^2}}, \quad A = \left(\text{Re}\text{tr}\mathbf{J}^{(\alpha)}\right)^2 - \left(3\text{tr}\mathbf{J}^{(\alpha)}\right)^2 - 4\text{Re}\det\mathbf{J}^{(\alpha)} \quad \text{and} \quad B = 2\text{Re}\text{tr}\mathbf{J}^{(\alpha)}\text{tr}\mathbf{J}^{(\alpha)} - 4\text{det}\mathbf{J}^{(\alpha)}.
\]

A straightforward but lengthy computation allows to rewrite the condition for instability Eq. (8) (main text), in terms of two polynomials, \( S_2 \) of second degree and \( S_1 \) of fourth degree. More precisely, \( S_2(\xi) = c_{2,2}\xi^2 + c_{2,1}\xi + c_{2,0} \) with coefficients

\[
c_{2,2} = -\det \mathbf{J}_2(4 \det \mathbf{J}_2 - (\text{tr}\mathbf{J}_2)^2)
\]
\[
c_{2,1} = \Delta_1(4 \det \mathbf{J}_2 - (\text{tr}\mathbf{J}_2)^2)
\]
\[
c_{2,0} = -\Delta_1^2 + \Delta_1\text{tr}\mathbf{J}_2 \text{tr}\mathbf{J}_2 - \det \mathbf{J}_2(\text{tr}\mathbf{J}_2)^2,
\]

and \( S_1(\xi) = c_{1,4}\xi^4 + c_{1,3}\xi^3 + c_{1,2}\xi^2 + c_{1,1}\xi + c_{1,0} \) with coefficients

\[
c_{1,4} = \det \mathbf{J}_2(\text{tr}\mathbf{J}_2)^2
\]
\[
c_{1,3} = \text{tr}\mathbf{J}_2(\Delta_1\text{tr}\mathbf{J}_2 + 2\det \mathbf{J}_2\text{tr}\mathbf{J})
\]
\[
c_{1,2} = \det \mathbf{J}(\text{tr}\mathbf{J}_2)^2 + 2\Delta_1\text{tr}\mathbf{J}_2 \text{tr}\mathbf{J}_2 + \det \mathbf{J}_2(\text{tr}\mathbf{J})^2
\]
\[
c_{1,1} = \text{tr}\mathbf{J}(2\det \mathbf{J}_2 \text{tr}\mathbf{J}_2 + \Delta_1\text{tr}\mathbf{J})
\]
\[
c_{1,0} = \det \mathbf{J}(\text{tr}\mathbf{J})^2,
\]

where we introduced \( \Delta_1 = J_{2,11}J_{22} - J_{2,12}J_{21} - J_{2,21}J_{12} + J_{2,22}J_{11} \).
Analysis of the Volterra model

As a first application of the method above introduced, we propose to study a Volterra model [27] that describes the interactions of preys, whose concentration is denoted by $y$, and predators, whose concentration is denoted by $x$, in an ecological setting. The Volterra model given by Eq. (9) admits a nontrivial fixed-point, $x^* = \frac{c_1 r - sd}{c_2 c_1^2}, y^* = \frac{a d}{c_1}$, which is positive and stable, provided that $c_1 r - sd > 0$. Consider now an ecosystem made of $n$ copies of the Volterra model, each copy representing a different ecological niche, $i = 1, \ldots, n$. And in the spirit of this work, let us assume that preys and predators interact at each node but also through long-range links; the latter can represent the ability of predators to exploit the presence of other predators sitting in nearby niches. Under the assumption of non-reciprocal interactions, $A_{ij} \neq A_{ji}$, several possible couplings are possible, we hereby study the one given by (10) (main text), that is

$$
\begin{align*}
\frac{dx_i}{dt} &= -dx_i + ac_1 y_i \frac{1}{k_{i1}^{\text{in}}} \sum_j A_{ij} x_j + (1-a)c_1 x_i \frac{1}{k_{i1}^{\text{in}}} \sum_j A_{ij} y_j \\
\frac{dy_i}{dt} &= ry_i - sy_i^2 - c_2 y_i \frac{1}{k_{i2}^{\text{in}}} \sum_j A_{ij} x_j,
\end{align*}
$$

(16)

By using the newly introduced Laplace matrix (3) (main text) we can rewrite the previous equations as:

$$
\begin{align*}
\frac{dx_i}{dt} &= -dx_i + c_1 y_i x_i + ac_1 y_i \sum_j L_{ij} x_j + (1-a)c_1 x_i \sum_j L_{ij} y_j \\
\frac{dy_i}{dt} &= ry_i - sy_i^2 - c_2 y_i x_i - c_2 y_i \sum_j L_{ij} x_j,
\end{align*}
$$

where one can easily recognise the in-node Volterra model (9) (main text) and the corrections stemming from non-local contributions.

As previously stated, the homogeneous solution $(x^*, y^*)$ is also a solution of the coupled system (16). Assuming this solution to be stable, we will prove in the following that it can be destabilised due to directed non-local coupling so driving the system towards a new heterogeneous, spatially dependent, solution. To prove this claim, we will linearise system (16) about the homogeneous equilibrium by setting $u_i = x_i - x^*$ and $v_i = y_i - y^*$ and then make use of the eigenbasis of the Laplace matrix $L$, $(\Lambda^{(\alpha)}, \phi^{(\alpha)})$, to project the linear system onto each eigenmode, that is

$$
\begin{align*}
\frac{d}{dt} \begin{pmatrix} u^\alpha \\ v^\alpha \end{pmatrix} &= \begin{pmatrix} (c_1 y^* - d) & c_1 x^* \\ -c_2 y^* & (1-a)c_1 x^* \end{pmatrix} + \Lambda^{(\alpha)} \begin{pmatrix} ac_1 y^* \\ -c_2 y^* \end{pmatrix} \\
&= (J + \Lambda^{(\alpha)} J_2) \begin{pmatrix} u^\alpha \\ v^\alpha \end{pmatrix} = J^{(\alpha)} \begin{pmatrix} u^\alpha \\ v^\alpha \end{pmatrix}.
\end{align*}
$$

(17)

By inserting the given expressions for $J$ and $J_2$, in the general formulas (14) and (15) we obtain for the coefficients of $S_2(\xi)$

$$
\begin{align*}
c_{2,2} &= -(a - 1)(c_1 r - ds) \left( \frac{4(a - 1)(c_1 r - ds)}{c_1} + a^2 d \right) \\
c_{2,1} &= (c_1 r(a - 2) + 2ds) \left( \frac{4(a - 1)(c_1 r - ds)}{c_1} + a^2 d \right) \\
c_{2,0} &= -(c_1 r(a - 2) + 2ds)^2 \left( \frac{c_1 r(a - 2) + 2ds}{c_1} \right) a ds + (a - 1)(c_1 r - ds)a^2 d,
\end{align*}
$$

and $S_1(\xi)$

$$
\begin{align*}
c_{1,4} &= -(a - 1)(c_1 r - ds)a^2 d \\
c_{1,3} &= ad \left( -(c_1 r(a - 2) + 2ds)a + 2s(a - 1)(c_1 r - ds) \right) \frac{1}{c_1} \\
c_{1,2} &= (c_1 r - ds)a^2 d + 2c_1 r(a - 2) + 2ds \frac{a}{c_1} ds - \frac{(a - 1)(c_1 r - ds)}{c_1^2} \frac{ds^2}{c_1^2} \\
c_{1,1} &= -ds \left( \frac{2c_1 r - ds}{c_1} a + \frac{c_1 r(a - 2) + 2ds}{c_1} s \right) \\
c_{1,0} &= \frac{c_1 r - ds}{c_1^2} ds^2.
\end{align*}
$$
FIG. 3: Instability region and patterns for the Volterra model. We report the region of the complex plane \((\Re \Lambda, \Im \Lambda)\) for which the instability condition is satisfied (grey), the instability is at play if at least one eigenvalue of \(L\) belongs to the region. The model parameters have been fixed to the values \(c_1 = 2, c_2 = 13, r = 1, s = 1, d = 0.02\) and \(a = 0.05\), and we can observe that the instability region intersects the real axis and thus both non-reciprocal (white dots) and reciprocal (black dots) interactions can exhibit eigenvalues entering into the instability region. This in turns implies the existence of an heterogeneous solution for both the reciprocal (see panel b) where we report the density of preys vs time) and non-reciprocal (see panel c) where we report the density of preys vs time) long-range interactions assumption. In both panels the horizontal black line denotes the homogeneous equilibrium \(y^*\).

Given such polynomials one can determine the (in)-stability region as shown in Fig. 1 (main text) or Fig. 3 and thus conclude about the onset of the instability according to the position of the complex eigenvalues of the Laplace matrix \(L\). In the latter Figure we indeed report the region of instability (grey) for a set of parameters values allowing for the emergence of patterns for both the reciprocal and non-reciprocal long-range interactions. We can observe that, contrary to the case shown in the main text, now the instability region has a non empty intersection with the real axis where lies the spectrum of the Laplace operator for reciprocal interactions (black dots). We can thus determine a web of symmetrical long-range interactions for which the Volterra model (9) (main text) exhibits an instability and eventually evolves toward a patchy solution (panel b) of Fig. 3. A similar result holds true using non-reciprocal long-range interactions, indeed the complex spectrum of the associated Laplace matrix (white dots in panel a) of Fig. 3 also lies in the instability region and thus the system converges to a spatially heterogeneous solution (panel c) of Fig. 3. In both cases, the system has been initialised \(\delta\)-close to the homogeneous equilibrium \((x^*, y^*)\) by drawing uniformly random perturbations in \((-\delta, \delta)\). Then its time evolution has been numerically simulated using a 4-th order Runge-Kutta method over a time span of the order of \(-\log \delta/\max \rho_\alpha\), namely sufficiently long to (possibly) increase the \(\delta\)-perturbation up to a macroscopic size. The underlying long-range coupling is a directed Erdős-Rényi network with \(n = 50\) nodes and a probability for a direct link to exist between two nodes is \(p = 0.5\).

In Fig. 4 we provide a more global view of the parameters range associated to bifurcation diagram showing the parameters values, \(d\) and \(c_1\), for which the instability emerges in the case of reciprocal interactions and non-reciprocal ones (black A region) and in the case of only non-reciprocal ones (white B region), once the remaining parameters have been fixed to some generic values. One can clearly appreciate how large is the latter compared to the former, and thus how more often one can find patterns due to non-reciprocal interactions instead of reciprocal ones.

**Analysis of the Stuart-Landau model**

We turn now our attention to the study of the paradigmatic model of nonlinear oscillators given by the Stuart-Landau system (SL) \[28, 29\]

\[
\frac{dw}{dt} = \sigma w - \beta |w|^2,
\]

where \(\sigma = \sigma_\mathbb{R} + i \sigma_\mathbb{I}\) and \(\beta = \beta_\mathbb{R} + i \beta_\mathbb{I}\) are complex model parameters. One can straightforwardly prove that \(w_{LC}(t) = \sqrt{\sigma_\mathbb{R}/\beta_\mathbb{R}} e^{i \omega t}\), \(\omega = \sigma_\mathbb{I} - \beta_\mathbb{I} \sigma_\mathbb{R}/\beta_\mathbb{R}\), is a limit cycle solution of the SL system and it is stable provided \(\sigma_\mathbb{R} > 0\) and \(\beta_\mathbb{R} > 0\).

We then assume to have \(n\) identical copies of the SL system coupled through non-reciprocal interactions, \(A_{\ell \ell} \neq A_{\ell i}\), and the hypothesis of mean field Eq. (12) (main text), hereby reported

\[
\frac{dw_i}{dt} = \frac{\sigma}{k_j^{(in)}} \sum_\ell A_{\ell \ell} w_\ell - \beta w_i |w_j|^2 = \sigma w_i - \beta w_i |w_j|^2 + \sigma \sum_\ell \mathcal{L}_{\ell \ell} w_\ell.
\]
FIG. 4: Bifurcation diagram for the Volterra model, reciprocal interactions. We fix the parameters values $c_2 = 13$, $r = 1$, $s = 1$ and $a = 0.05$, and we show the bifurcation region as a function of the remaining parameters $d$ and $c_1$. The C region (grey) corresponds to an unstable homogeneous equilibrium that also remain unstable once the coupling is present, being the latter reciprocal or non-reciprocal; patterns can develop but they are not due to the interactions. For parameters values in the A region (black), the stable homogeneous equilibrium is destabilised by the introduction of reciprocal coupling (as well by a non-reciprocal one); the patterns shown in the panel b) of Fig. 3 associated to the values $c_1 = 2$ and $d = 0.02$ fall in this class (yellow dot). Finally in the large B region (white) the homogeneous equilibrium is stable for any reciprocal coupling, and thus no pattern can develop in this case, however the use of non-reciprocal interactions can drive the instability and thus the emergence of patterns. The patterns shown in the panel b) of Fig. 3 (main text) correspond to the values $c_1 = 2$ and $d = 0.4$ clearly belonging to the B region (blue star).

Because of the structure of the coupling, $w_{LC}(t)$ is also a solution of the latter equation. To inquire about its stability we consider the perturbation given by $w_j(t) = w_{LC}(t) (1 + u_j(t)) e^{i v_j(t)}$, where $u_j(t)$ and $v_j(t)$ are real and small functions nodes dependent. We then insert the latter into (12) (main text) and we expand by retaining only the first order terms by obtaining

$$\frac{d}{dt} \begin{pmatrix} u_j \\ v_j \end{pmatrix} = \begin{pmatrix} -2\sigma_R & 0 \\ -2\beta_3 \sigma_R & 0 \end{pmatrix} \begin{pmatrix} u_j \\ v_j \end{pmatrix} + \sum L_{j\ell} \begin{pmatrix} \sigma_R & -\sigma_3 \\ -\sigma_3 & \sigma_R \end{pmatrix} \begin{pmatrix} u_\ell \\ v_\ell \end{pmatrix}.$$  \hfill (18)

We invoke once again the existence of a orthonormal eigenbasis of the Laplace matrix, $\phi^{(\alpha)}$, $\Lambda^{(\alpha)}$, to decompose the perturbation $u_j$ and $v_j$, and eventually get

$$\frac{d}{dt} \begin{pmatrix} u^\alpha \\ v^\alpha \end{pmatrix} = \left( \begin{pmatrix} -2\sigma_R & 0 \\ -2\beta_3 \sigma_R & 0 \end{pmatrix} + \Lambda^{(\alpha)} \begin{pmatrix} \sigma_R & -\sigma_3 \\ -\sigma_3 & \sigma_R \end{pmatrix} \right) \begin{pmatrix} u^\alpha \\ v^\alpha \end{pmatrix} = \left( J + \Lambda^{(\alpha)} J_2 \right) \begin{pmatrix} u^\alpha \\ v^\alpha \end{pmatrix} =: J^{(\alpha)} \begin{pmatrix} u^\alpha \\ v^\alpha \end{pmatrix}.$$  \hfill (19)

By inserting the given expressions for $J$ and $J_2$, in the general formulas we obtain for the coefficients of $S_2(\xi)$

$$c_{2,2} = -\sigma_3^2 (\sigma_R^2 + \sigma_3^2)$$
$$c_{2,1} = 2\sigma_3^2 \sigma_R (\beta_3 \sigma_R + \beta_3 \sigma_3) \frac{1}{\beta_R}$$
$$c_{2,0} = -\sigma_3^2 \sigma_R^2 (\beta_R^2 + \beta_3^2) \frac{1}{\beta_R^2},$$  \hfill (20)

while for $S_1(\xi)$

$$c_{1,4} = \sigma_R^2 (\sigma_R^2 + \sigma_3^2)$$
$$c_{1,3} = -2\sigma_R^2 (2\beta_R \sigma_R^2 + \beta_3 \sigma_R \sigma_3 + \beta_3 \sigma_R^2) \frac{1}{\beta_R}$$
$$c_{1,2} = \sigma_R^2 (5 \beta_R \sigma_R^2 + 4 \beta_3 \sigma_R \sigma_3 + \beta_R \sigma_R^2) \frac{1}{\beta_R^2}$$
$$c_{1,1} = -2\sigma_R^2 (\beta_R \sigma_R + \beta_3 \sigma_3) \frac{1}{\beta_R}$$
$$c_{1,0} = 0.$$  \hfill (21)
FIG. 5: Instability region and patterns for the Stuart-Landau model. In panel a) we report the region of the complex plane ($\Re \Lambda, \Im \Lambda$) for which the instability condition is satisfied (grey), for the parameters values $\sigma_R = 1$, $\sigma_I = 4.3$, $\beta_R = 1$ and $\beta_I = -2$. We can observe that the instability region intersects the real axis and thus any kind of coupling, being reciprocal (black dots) or non-reciprocal one (white dots), can exhibit eigenvalues entering the instability region and thus allowing for an instability to set on, followed by a spatio-temporal patterns as shown in panel b) where we report the real part of the complex state variable $w_i$ in the case of a reciprocal coupling and panel c) for a non-reciprocal one).

FIG. 6: Bifurcation diagram for the Stuart-Landau model. For the set of parameters values $\sigma_R = 1.0$ and $\beta_R = 1.0$ we report the range of the remaining parameters $\sigma_I$ and $\beta_I$ for which the instability can emerge. In the region A (black) the homogeneous equilibrium is stable and it can be destabilised by a reciprocal coupling as well by a non-reciprocal one. On the other hand, in the B region (white), the homogeneous equilibrium is always stable, no pattern can develop using a symmetric coupling. On the contrary one can found non-reciprocal coupling capable to destabilise the homogeneous equilibrium and thus the system to develop a wavy heterogeneous solution. The patterns shown in the panel b) of Fig. 2 (main text) correspond to the values $\sigma_I = 4$ and $\beta_I = 1$ and clearly belong to the B region (blue star). The patterns presented in Fig. 5 for parameters values $\sigma_I = 4$ and $\beta_I = -2$ correspond to the region A (yellow dot). The numerical simulations have been perfumed using a 4-th order Runge-Kutta method starting from initial conditions $\delta$-close to the homogeneous limit cycle solution $w_{LC}(t) = \sqrt{\sigma_R / \beta_R} e^{i \omega t}$. In both cases the maximum of the dispersion relation $\rho_\alpha$ is of order of the unity and thus a relatively small integration span is sufficient to reveal the wavy solution. The underlying coupling is a directed Erdős-Rényi network with $n = 40$ nodes and a probability for a direct link to exist between two nodes is $p = 0.08$.

As previously done in the case of the Volterra model, the explicit knowledge of the polynomial $S_1$ and $S_2$ allows to compute the (in)-stability region as shown in Fig. 2 (main text) or Fig. 5 in a setting where the instability condition can be realised for both a reciprocal and non-reciprocal coupling. The instability region (grey) is shown in the complex plane ($\Re \Lambda, \Im \Lambda$) together with the spectrum of a reciprocal web of long-range interactions (black dots) as well with a non-reciprocal one (white dots); because in both cases there are eigenvalues belonging to the instability region, the instability is possible and thus a spatio-temporal pattern emerges (see panel b) in the case of reciprocal can and panel c) for the non-reciprocal one). The numerical simulations have been performed using a 4-th order Runge-Kutta method starting from initial conditions $\delta$-close to the homogeneous limit cycle solution $w_{LC}(t) = \sqrt{\sigma_R / \beta_R} e^{i \omega t}$. In both cases the maximum of the dispersion relation $\rho_\alpha$ is of order of the unity and thus a relatively small integration span is sufficient to reveal the wavy solution. The underlying coupling is a directed Erdős-Rényi network with $n = 40$ nodes and a probability for a direct link to exist between two nodes is $p = 0.08$.

In Fig. 6 we report the bifurcation diagram in the plane $\sigma_\beta$ and $\beta_\beta$, for $\sigma_R = \beta_R = 1$. Two regions can be observed; in region A (black) the instability can be initiated by both a reciprocal and non-reciprocal web of long-range interactions while in region B (white) only non-reciprocal interactions can determine an instability and the ensuing wavy solution.
About the spectrum of the reactive Laplacian in case of reciprocal interactions.

Let us assume the network of interactions to be symmetric, \( A_{ij} = A_{ji} \), for all \( i \) and \( j \), and let us recall the definition of the reactive Laplacian \( L_{ij} = A_{ij}/k_i - \delta_{ij} \), where \( k_i = \sum_j A_{ij} \), is the node degree. Let us introduce the symmetric Laplace matrix \( L_{ij}^{\text{sym}} = A_{ij}/\sqrt{k_i k_j} - \delta_{ij} \) and observe that its eigenvalues are real and negative but the null one. Let \( D \) be the diagonal matrix with the nodes degree on the diagonal, then

\[
L = D^{-1}A - I = D^{-1/2} \left[ D^{-1/2} A - I \right] D^{1/2} = D^{-1/2} L^{\text{sym}} D^{1/2}.
\]

Namely \( L \) and \( L^{\text{sym}} \) are similar matrices and thus exhibit the same set of eigenvalues.