Mesoscale symmetries explain dynamical equivalence of food webs

Helge Aufderheide¹, Lars Rudolf and Thilo Gross
University of Bristol, Merchant Venturers School of Engineering, Bristol, UK
E-mail: he.adh@biond.org

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Abstract. A goal of complex system research is to identify the dynamical implications of network structure. While early results focused mainly on local or global structural properties, there is now growing interest in mesoscale structures that comprise more than one node but not the whole network. A central challenge is to discover under what conditions the occurrence of a specific mesoscale motif already allows conclusions on the dynamics of a network as a whole. In this paper, we investigate the dynamics of ecological food webs, complex heterogeneous networks of interacting populations. Generalizing the results of MacArthur and Sánchez-García (2009 Phys. Rev. E 80 26117), we show that certain mesoscale symmetries imply the existence of localized dynamical modes. If these modes are unstable the occurrence of the corresponding mesoscale motif implies dynamical instability regardless of the structure of the embedding network. In contrast, if the mode is stable it means that the symmetry can be exploited to reduce the number of nodes in the model, without changing the dynamics of the system. This result explains a previously observed dynamical equivalence between food webs containing a different number of species.

¹ Author to whom any correspondence should be addressed.
1. Introduction

When analysing complex systems, a central question is whether one can find a reduced representation that exhibits the same phenomena, but is easier to handle mathematically. Networks offer a conceptual framework that facilitates this reduction [1–4]. By representing the system as a set of discrete nodes connected by links, networks neglect much of the internal complexity of the system’s constituents, but retain the complexity of their interaction. Thereby, they offer a suitable intermediate level of description on which a qualitative understanding of the systems dynamics can be gained.

In this paper, we consider specifically the example of ecological food webs [5], i.e. the networks of who-eats-who in ecology. In these networks, the nodes represent distinct populations, whereas the links represent predator–prey interactions. Food web models offer a highly simplified description of ecological systems, often characterizing the state of a population by a single variable, and neglecting for instance non-predatory interactions and intra-population dynamics. However, they capture the complexity of the network of predatory interactions that forms the backbone of most natural ecosystems [6–13].

A detailed analysis of food web dynamics, typically comprising 50–500 populations on time scales from hours to decades, poses a considerable challenge. Thus, one often considers coarse-grained models in which different populations are grouped and represented by one aggregate variable, thereby creating a trade-off between the degree of simplification and approximation precision [14–16].

A classical example of aggregation is food chain models in which whole layers of the food web such as phytoplankton, zooplankton or fish are described by a single variable, respectively [17]. More biological information is preserved by aggregating the so-called functional groups or guilds comprising species which are similar in morphology, life strategy or niche [14, 18, 19]. For instance, the ERSEM model [20] distinguishes four groups of phytoplankton for the North Sea, three of them defined by body size and one comprising all species with a silicate shell.

As an alternative strategy, it has been proposed to aggregate those species that hold similar topological positions in the network [21–24], such as sharing similar prey and predators [25]. Recent work [22, 23, 26] focuses on the identification of strongly connected groups, known as communities in network terminology (in contrast to the ecological usage of the term). Such
communities are identified automatically by community detection algorithms [24]. One then builds on the idea that dynamics within the community should equilibrate more rapidly than the dynamics that couple the community to the rest of the net. A reasonable approximation is then to neglect the internal dynamics and represent the community by a single aggregate variable.

From a theoretical perspective, the problem of coarse-graining networks is interesting because it touches upon mesoscale network properties. We seek to identify a set of nodes that are sufficiently similar, such that their aggregation induces only minor changes in the dynamics. Apart from community detection [22–24], the mesoscale properties of food webs have previously been studied in terms of motif distributions [27–29]. In this context a motif is a small set of nodes and their interactions. The statistical over- or under-representation of certain motifs is thought to have implications for the network functioning. Applied to food webs, it was shown [28] that a certain three-node motif has a destabilizing effect, but implications of other motifs remain mostly uncertain and no theory on the dynamical implications of motifs has been formulated.

The ultimate goal of coarse graining is to find a reduced representation of the network that exactly captures the relevant dynamics of the system and possibly even allows us to re-establish the complete system dynamics. This goal is generally hard to achieve as it seems to imply knowledge of the dynamics of the original system. However, in a recent publication [30] it was shown in a class of generalized models (GMs) [31, 32] that under certain conditions an aggregation is possible that conserves the local dynamics around steady states and at least certain features of the global dynamics exactly. Although the previous paper demonstrated this aggregation in several examples, it failed to provide a detailed analysis of the underlying symmetries that make the aggregation possible.

In this paper, we build on recent advances [33] in studying the implications of graph orbits, which capture the mesoscale symmetries in the network structure. Extension of the results in [33] to directed and weighted networks allows application of them to study the food web dynamics. This reveals the topological mechanism of the reduction rule identified heuristically in [30] and provides more general rules for food web aggregation. We note that the previously observed identity is of limited use for the analysis of food web data. However, its theoretical investigation provides an example of mesoscale structures having distinct implications for the network dynamics.

The paper starts, in section 2, with a brief review of previous results. In section 3, we introduce the notion of symmetries in food webs, and show that symmetric nodes carry localized dynamical modes that are sensitive solely to the symmetric structure and thus independent of the embedding network. In section 4, we compute these modes for several example symmetries and derive exact coarse-graining rules exploiting the symmetry. The implications of these results are discussed in section 5.

2. Dynamical equivalence of food webs

The application considered below builds on previous results obtained with a GM of ecological food webs [31, 32]. In this section, we provide an overview of the approach to generalized modelling and previous results on food web stability.

A GM is a system of differential equations in which not all the processes are restricted to specific functional forms [31]. For instance, the food web model studied below describes the dynamics of the biomass belonging to $N$ populations $X_1, \ldots, X_N$ by $N$ differential equations
of the form
\[
\frac{d}{dt} X_i = G_i(X) + S_i(X_i) - L_i(X) - M_i(X_i),
\]
where \(G_i, L_i, M_i\) and \(S_i\) are unspecified functions describing gains due to predation, loss due to predation, loss due to natural mortality and gain due to primary production, respectively.

GMs are typically too general to compute the number or location of steady states without further assumptions. However, they can be analysed by local stability analysis. For this purpose, we assume that a steady state \(X^* = (X^*_1, \ldots, X^*_N)^T\) were known and then formally linearize the system around this unspecified steady state. The coefficients of the linearized system can be expressed by the Jacobian matrix, \(J_{ij} = \frac{\partial}{\partial X_j} \left( \frac{d}{dt} X_i \right) |^*\), which depends on the derivatives of the unspecified functions in the model. For instance, in the food web model this unspecified information appears in expressions such as \(\frac{\partial G_i}{\partial X_i} |^*\). This derivative describes an unknown but constant quantity or, in other words, an unknown scalar parameter of the system. Because this parameter is hard to interpret, we use a slightly different parameterization, which is obtained either by a special normalization procedure \([31]\) or directly by the identity
\[
\frac{\partial G_i}{\partial X_i} |^* = \frac{G_i^*}{X_i^*} \frac{\partial \log G_i}{\partial \log X_i} |^*,
\]
which is true for \(G_i^*, X_i^* > 0\) (a condition that is generally met by definition; the special case of \(X_i^* = 0\) is discussed in \([34]\)).

The expression on the right-hand side of (2) is a product of two factors that can be interpreted directly in most applications. The first factor is a per-capita rate. Such rates have the dimension of inverse time and can be directly interpreted as characteristic turnover rates, i.e. the inverse of the mean life expectancy of individuals. The second factor is a logarithmic derivative. Such derivatives are also called elasticities and have been proposed originally in economic theory \([35]\) and are also used in the context of metabolic control theory \([36]\). They can be estimated well from the data and interpreted straightforwardly. For every power law, \(f(x) = Ax^p\), the logarithmic derivative is \(\frac{\partial \log f}{\partial \log x} = p\), independently of \(A\) or \(x\). Thus, for instance, any linear function has an elasticity of one, regardless of the slope. For functions that are not power laws the elasticity still provides an intuitive nonlinear measure of the sensitivity in the steady state.

From the parameterized Jacobian the dynamics close to the steady state under consideration can be computed. The steady state is stable if all eigenvalues of the Jacobian have negative real parts \([37]\). Stability is lost when a change of parameters causes at least one eigenvalue to cross the imaginary axis, leading to a local bifurcation. Because the Jacobian is a real matrix the eigenvalues in question can be either real or form a complex conjugate eigenvalue pair. In the former case a bifurcation of saddle-node type occurs in which the number of steady states changes. In the latter case a Hopf bifurcation occurs which marks the onset of oscillations (in the supercritical case) or the disappearance of an unstable limit cycle (in the subcritical case) around the steady state leading to transitory but generally unstable oscillations.

The mathematical validity of generalized modelling was recently confirmed by rigorous proofs \([34]\), whereas applicability to actual problems from different fields was demonstrated in several recent publications \([32, 38–44]\).

A GM for ecological food webs \([31]\) was used in \([30]\) to study critical points in parameter space in which the dynamics around steady states changes in bifurcations. The authors noted
The bifurcation diagrams of different food web models are exactly identical if plotted as a function of the generalized parameters, as shown in the three-parameter bifurcation diagrams in the top row. The parameter space in this example is spanned by three generalized parameters denoting the nonlinearity of mortality $m$, the sensitivity of predators to prey abundance $g$, and the ratio between the time scales of predator and prey dynamics $r$. Every point in the parameter space corresponds to a specific steady state. The surfaces in the diagrams mark the location of bifurcation points of Hopf (red, green) and saddle-node (blue) bifurcations. Steady states are stable if they lie in the front volume of the bifurcation diagram. The two diagrams correspond to different food webs, indicated symbolically in the corner. In the symbolic representation, nodes indicate populations and arrows indicate biomass flows due to predator–prey interactions. Using this notation the dynamical equivalence conjectured in [30] is shown symbolically in the lower row.

The main conclusion of the previous paper [30] can be summarized in the conjecture that two species that (i) interact with the same set of topological neighbours and (ii) are described by the same generalized parameters can be aggregated into a single variable without changing the local bifurcation points.

We note that the conjectured identity of bifurcation diagrams is not trivially true because of the nonlinearity of the underlying equations. Indeed, the identity is much harder to observe in conventional models and hence was not noted before the publication of [30].
Finally, consider that the identity extends also to local bifurcations of higher codimension (found, for instance, at the intersections of bifurcation surfaces) that have implications for the global dynamics of the system [37, 45]. So the proposed aggregation must also conserve at least some features of the global dynamics.

3. Mathematical treatment of symmetries

The equivalence of food webs described above is contingent on the presence of a specific symmetry in the topology of the food web. In particular, an equivalent reduction of the network was found to be possible if at least two populations in the network interacted with exactly the same neighbours.

In this section, we review and extend previous results on the implications of symmetries in networks. Furthermore, we introduce the terminology that is used below for establishing a formal link between mesoscale symmetries and dynamics. We note that our presentation follows in many parts the paper [33], but extends the theory presented therein to directed networks.

The key concept to define graph symmetries is node permutations. For instance, to permute two nodes \( n_1 \) and \( n_2 \), all links previously connecting to \( n_1 \) are rewired to \( n_2 \) and all links previously connecting to \( n_2 \) are rewired to \( n_1 \). We note that permutations may involve more than two nodes, allowing us for instance to exchange two pairs of nodes at the same time. Formally, the structure of a network with \( N \) nodes, \( n_1, \ldots, n_N \) is commonly represented by the adjacency matrix \( A \), which is an \( N \times N \) matrix with \( A_{ij} = 1 \) if there is a directed link from \( n_i \) to \( n_j \) and \( A_{ij} = 0 \) otherwise. We say that a network contains a symmetry represented by a permutation matrix \( P \) when the application of this permutation leaves the adjacency relations unchanged, i.e. \( PA = A \).

We note that if multiple symmetries exist they can be combined into larger symmetries, e.g. by an element-wise addition of the corresponding permutation matrices. For simplicity we will therefore limit ourselves to symmetries that are minimal such that they cannot be decomposed into symmetries permuting on fewer nodes. In the following, we denote all nodes that participate in a given minimal symmetry as a symmetric structure. Further, a set of nodes that are mapped onto each other under a minimal symmetry operation is said to form an orbit.

In the simplest case a symmetric structure contains only one such orbit (figure 2(a)). However, some symmetric structures comprise multiple orbits such that multiple nodes have to be exchanged in parallel in order to preserve adjacency (figure 2(b)).
We refer to the number of nodes belonging to an orbit as the size of the orbit. The size is the number of identical graphs generated by the corresponding symmetry operation unless a symmetric structure contains nested orbits (figure 2(c)).

Although the concept of orbits was originally proposed for unweighted networks, it can be intuitively extended to weighted nets. In this case we additionally demand that symmetries conserve link direction and weight, such that the corresponding permutation leaves the matrix of link weights unchanged.

In [33], it is shown that symmetries in undirected networks have a distinct impact on the spectrum of the adjacency matrix. In particular, if a symmetric structure is present, then the eigenvalues can be decomposed into two classes. The first class contains the so-called redundant eigenvalues. These eigenvalues correspond to eigenvectors that are localized on the symmetric structure. The second class contains all other (non-redundant) eigenvalues. The eigenvectors corresponding to non-redundant eigenvalues have identical values in all elements that correspond to nodes in the same orbit. These results suggest that reducing the network by collapsing all nodes in each orbit onto each other leaves the spectrum of the adjacency invariant, except for removing the redundant eigenvalues.

In the following, we show that very similar results can be obtained for the Jacobian matrix of the food web model. This allows us to identify situations where the number of nodes can be reduced while leaving the spectrum of the Jacobian unchanged except for the removal of redundant eigenvalues. When the redundant eigenvalues have a negative real part the resulting reduction leads to a lower-dimensional, but dynamically equivalent, system. To establish this reduction we consider the Jacobian as the adjacency matrix prescribing the weights and directions of the links in a (hypothetical) network.

We note that for food webs the network prescribed by the Jacobian matrix is not identical to the network of predator–prey interactions. For instance, additional mutualistic interactions arise in the Jacobian matrix between the prey populations of a given predator [31]. The interactions originate from an effect called apparent competition, in which the presence of one prey species leads to a decreased predation on another prey because of nonlinearities in the predation kinetics. Nevertheless, if species belong to an orbit in the network of predator–prey interactions and if their generalized parameters are identical, then they also form an orbit in the network defined by the Jacobian matrix. We therefore only have to show that the results of [33] can be extended to weighted and directed networks.

Following [33], we argue that each symmetry generates an invariant subspace \( V \) of the Jacobian matrix, which contains only vectors \( v \) that are localized on the symmetric structure, such that all elements corresponding to nodes outside the symmetric structure are zero. This subspace \( V \) then acts as the foundation for the set of eigenvectors that are localized on the symmetric structure.

To prove the existence of that subspace \( V \), we must show that there is a non-empty set of localized vectors \( v \) that are in \( V \) and remain in \( V \) under the application of the Jacobian matrix, such that \( Jv \in V \). We now show that these conditions are met by vectors defined as follows: given a symmetric structure, let \( V \) include all vectors that are zero in elements corresponding to nodes outside the symmetric structure (localization condition), and for which the elements that correspond to nodes in the same orbit sum to zero (zero-sum condition).

We now show that for any \( v \) that obeys the condition above, application of the Jacobian leads to a vector \( z = Jv \), which still meets the zero-sum and localization conditions and thus
lies within $V$. To show that $z$ obeys the localization condition let us consider a node $k$ outside the symmetric structure. We compute the component of $z$ in $k$ as $z_k = S_0 + \sum_j S_j$. Here all of the terms $S_j$ have the structure $S_j = \sum_i J_{ki} v_i$, but the summation runs over all $i$ that correspond to nodes outside the symmetric structure for $j = 0$ and over all $i$ that correspond to nodes in orbit $j$ otherwise. Now consider that all terms in $S_0$ are products of $v_i$, where $i$ is outside the symmetric structure, and are hence zero because $v$ obeys the localization condition. Thus $S_0 = 0$. Regarding the other terms $S_1, S_2, \ldots$, consider that symmetry implies that node $k$ must be connected to all nodes in an orbit with the same connection weight $J_{ki} = b$. Therefore, $S_j = \sum_i J_{ki} v_i = b \sum_i v_i = 0$, where we used in the final step that the summation runs over all $v_i$ belonging to the same orbit, which is zero because $v$ obeys the zero-sum condition. Thus for all terms $S_j = 0$ individually and hence $z_k = 0$, which shows that $z$ meets the localization condition.

Secondly, we have to show that $z$ meets the zero-sum condition. For this purpose let us consider the connections of an orbit $p$ with the nodes of an orbit $q$ under the action of the Jacobian. One can always find a reordering of the variables such that all terms representing the links from nodes in $p$ towards nodes in $q$ appear in a single block in $J$. In the following, we refer to such blocks as orbit connections and denote them by $C^{qp}$.

First we show that the sum over the elements of $C^{qp} v$ belonging to nodes in $q$ is zero. We can write this sum as $\sum_i (C^{qp} v)_i$, where $i$ runs over the nodes in $q$ (over all elements of the vector $C^{qp} v$). However, this is identical to first taking the sum over the elements of each column of $C^{qp}$ and then multiplying by the vector $v$. The column sums of $C^{qp}$, respectively, correspond to the sum over all links originating from one node in $p$ and are therefore identical by symmetry. Let this sum be $c$. We can then write $\sum_i (C^{qp} v)_i = c \sum j v_j = 0$, where $i$ runs over nodes in $q$ and $j$ runs over all nodes in $p$. In other words, this shows that the sum of the input that a given orbit receives from any other orbit under the application of the Jacobian on a vector in $V$ sums to 0. As the vector $z$ is a sum of such contributions, $z$ must meet the zero-sum condition.

Because both localization and the zero-sum condition are met by $z$, $V$ is an independent subspace under $J$. In the following, we call this subspace the redundant subspace of the corresponding symmetry. We note that the redundant subspace of a symmetry of $o$ orbits and of size $s$ has dimension $o(s - 1)$. Further, the compliment of the redundant subspace $W = V^\perp$ is also an independent subspace. The orthogonality of $W$ and $V$ implies that any vector $w$ in $W$ is constant on nodes belonging to the same orbit.

Intuitively speaking, the above reasoning shows that all eigenmodes of the Jacobian fall into two categories: those that affect symmetric nodes anti-symmetrically and those that affect symmetric nodes symmetrically. The redundant subspace $V$ contains eigenmodes affecting symmetric nodes anti-symmetrically. Thus the effect on nodes outside the respective symmetric structure cancels, which explains the localization. The subspace $W$ contains eigenmodes affecting the symmetric nodes symmetrically. Thus the effect on nodes outside the symmetric structure does not cancel and couples the orbit to the rest of the system.

So far we have shown that the presence of a symmetric structure can be linked directly to the redundant eigenvalues in the spectrum of the Jacobian. These eigenvalues and the corresponding eigenvectors correspond to local eigenmodes governing the approach or departure of the system to or from the steady state. Therefore symmetric structures provide a rare example of mesoscale motifs that have exactly prescribed implications for the system-level dynamics, which are independent of the structure of the embedding network.
To compute the redundant eigenvalues, one needs to diagonalize the Jacobian only in the subspace $V$. The difficulty involved thus depends on the complexity of the symmetric structure, but not on the complexity of the embedding system. Further knowing that the eigenvectors have entries that obey the zero-sum condition on every orbit makes the computation of eigenvalues particularly easy.

One can now imagine a mapping which collapses all nodes in a given orbit onto each other such that each orbit is replaced with a single substitute node. It is intuitive that such a mapping should remove the redundant eigenvalues from the spectrum of $J$ while leaving all other eigenvalues unchanged. For confirmation we write $J$ for vectors inside $Z$ in terms of new variables $w'^p$, each of which replaces all the (identical) variables of an orbit $p$. We recall that this substitution is possible because vectors in $W$ are constant on each orbit.

More explicitly, the elements of the vector $Jw$ corresponding to nodes of given orbit $q$ are given by $\sum_p C^{qp} 1 w'^p$, where $p$ runs over all orbits, $C^{qp}$ denotes the orbit connection from $p$ to $q$, and $1$ is a vector that contains the entry 1 for each node in $p$. Because each of the row-sums of $C^{qp}$ represents the sum over the incoming links of one node in $q$ from nodes in $p$, the entries of $C^{qp} 1$ representing these row-sums are identical. We can therefore consistently replace the entries in $\sum_p C^{qp} 1 w'^p$ by $w'^q$. Hence the connection from the variables $w'^p$ to $w'^q$ is given by the row-sum of $C^{qp}$. This defines the reduced Jacobian matrix $J'$, which contains at each position this connection from $w'^q$ to $w'^p$. Furthermore, it defines the reduced (hypothetical) network of $J'$ which contains one node for each replacement variable ($w'^p$ instead of the orbit $p$), confirming the intuitive assumption.

These results can be summarized in a simple algorithm which reduces the Jacobian, but leaves its spectrum unchanged except for removing the redundant eigenvalues. Starting with a network representation of the Jacobian $J$, we remove all symmetric nodes except one from each orbit. Links that pointed towards a removed node are removed and links originating from a removed node are rewired such that they originate from the remaining node in the same orbit. Finally, we simplify the network by replacing all links originating and ending in the same nodes by a single new link. The weight of this new link is the sum over the replaced ones.

The spectrum of the reduced Jacobian matrix $J'$ describes the dynamics of the original system, except for the localized redundant part. However, if the redundant eigenvalues of $J$ have a negative real part, they do not change the dynamics qualitatively and the dynamics described by $J'$ are equivalent to the dynamics described by $J$.

Once the Jacobian has been equivalently reduced, one can try to construct a physical representation of the reduced system. We illustrate this process for food webs in the next section.

4. Application to food webs

The results in section 3 imply that the nodes belonging to a symmetric structure in a food web carry localized dynamical modes. Reducing the food web model by collapsing the symmetric nodes removes the localized modes associated with the symmetry but leaves the remaining dynamical modes intact. Thus this reduction leads to an equivalent dynamical system if the removed modes are stable, i.e. when the redundant eigenvalues have negative real parts. In this section we illustrate these results by analysing different symmetric structures in example food webs.

We start by considering the so-called competitive-exclusion motif shown in figure 3(a). In this motif two top-predators (populations 1, 2) feed on the same prey (population 3). Using [32]
the stability of any steady state in such a food web is governed by a Jacobian of the form

\[
J = \begin{pmatrix}
J_{11} & 0 & J_{13} \\
0 & J_{22} & J_{23} \\
J_{31} & J_{32} & J_{33}
\end{pmatrix}.
\] (3)

This motif contains a symmetry if the generalized parameters of populations 1 and 2 are identical (such that \(J_{13} = J_{23}, J_{11} = J_{22}, J_{31} = J_{32}\)). Simple diagonalization then yields the three eigenvalues \(\lambda_3 = J_{11}\) and \(\lambda_{1,2} = \frac{1}{2}(J_{11} + J_{33} \pm \sqrt{\Delta})\), where \(\Delta = (J_{11} - J_{33})^2 + 4J_{31}J_{33}\).

Following the procedure outlined in the previous section, we can write the Jacobian of a smaller system

\[
\tilde{J} = \begin{pmatrix}
J_{11} & J_{13} \\
2J_{31} & J_{33}
\end{pmatrix},
\] (4)

which exhibits qualitatively similar dynamics. Straightforward diagonalization confirms that this reduced matrix \(\tilde{J}\) retains eigenvalues \(\lambda_{1,2}\), while the eigenvalue \(\lambda_3\) corresponding to the mode associated with the mesoscale symmetry has disappeared.

We note that the reduced matrix \(\tilde{J}\) can be interpreted as the Jacobian of a predator–prey system. This is not trivial because terms such as \(J_{13}\) and \(J_{31}\) are not independent, but can be expressed as functions of the same set of generalized parameters. Using the detailed representation of these terms [30, 45] we verified (see appendix A) that \(\tilde{J}\) corresponds to a predator–prey system, in which the prey is described by the same parameters as species 3 in the original system and the predator by the parameters of species 1. It is remarkable that the factor 2 in \(\tilde{J}\) that arises from the reduction is indeed needed to make this direct correspondence possible.

**Figure 3.** Examples of food webs that differ only by dynamical modes localized inside their mesoscale symmetries. Different colours denote different orbits. Two systems are marked as dynamically equivalent (‘=’) if the spectra of their Jacobian matrices are identical up to the eigenmodes characterizing the mesoscale effects inside the symmetries. If nodes of a symmetry have a common prey or predator with a node outside the symmetry, such as e.g. in (i), the generalized parameters of the common prey or predator in the reduced network are weighted, which is shown in (j) as a double-headed link. See text for more details.
The dynamics of the reduced (predator–prey) system is equivalent to the original (competitive-exclusion) system if the dynamics in the direction of the redundant eigenvector is stable, i.e. if the eigenvalue $\lambda_3$ that disappears in the reduction has a negative real part. For the competitive-exclusion motif this is typically the case when the predators suffer from super-linear mortality [46].

While we have so far focused on the three-node web for illustration, we emphasize that the same reduction can be applied in food webs of arbitrary size. In particular, using the results from the previous section, it is not necessary to compute the complete spectrum of the Jacobian to apply the reduction. For instance, consider the competitive-exclusion motif that appears in the web carries the redundant eigenvector associated with the eigenvalue $\lambda_3$ found before. Removing the associated dynamical modes leads to the Jacobian matrix of the reduced food web in figure 3(e), which is dynamically equivalent if $\lambda_3 < 0$.

As a second example we consider the so-called apparent-competition motif shown in figure 3(c), i.e. one predator (population 1) feeding on two prey species (populations 2, 3). The Jacobian matrix is

$$\mathbf{J} = \begin{pmatrix} J_{11} & J_{12} & J_{13} \\ J_{21} & J_{22} & J_{23} \\ J_{31} & J_{32} & J_{33} \end{pmatrix},$$

where we have assumed that the prey species are described by identical ecological parameters. In contrast to the Jacobian of the competitive-exclusion motif this matrix contains the elements denoted by $J_{23}$ that couple the symmetric (prey) species. These are the mutualistic apparent competition terms that were already mentioned above.

The dynamical mode localized on the two prey species corresponds to the eigenvector $(0, 1, -1)^T$ and thus to the eigenvalue $\lambda_3 = J_{22} - J_{23}$. Therefore if $J_{22} < J_{23}$, which is generally the case in food webs, then removing the dynamical mode of the symmetry leads to a dynamically equivalent system.

Following the procedure outlined in section 3, we can write the Jacobian of the reduced system as

$$\mathbf{\tilde{J}} = \begin{pmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} + J_{23} \end{pmatrix},$$

which retains the eigenvalues of $\mathbf{J}$ except for $\lambda_3$. Comparing $\mathbf{\tilde{J}}$ to the Jacobian matrix of the system in figure 3(b), we find that $\mathbf{\tilde{J}}$ describes a predator–prey system with identical generalized parameters (see appendix B).

The other examples in figure 3 can be treated along the same lines as above. Let us therefore comment only briefly on two new features that appear. Firstly, when aggregating symmetric species that share a common predator with other species that are not part of the same orbit, care has to be taken that the aggregate species enters with correct weight. For instance in figure 3(i), if we assume that the top predator receives two-thirds of its biomass from the two symmetric species. Then in the reduced system the species replacing the orbit has twice the weight in comparison to the non-symmetric prey on the right.
Secondly, we note that symmetries consisting of more than one orbit may exhibit more complicated localized dynamics. Still, calculation of the eigenvalues for a given structure is straightforward because the structure of the localized eigenvectors is prescribed by the zero-sum conditions for each orbit. For instance, in the food web shown in figure 3(h) the symmetric structure consists of two interconnected orbits. The redundant eigenvectors therefore take the structure $v = (a, -a, b, -b, 0)^T$, such that the entries $a, -a$ satisfy the zero-sum condition on the first orbit and $b, -b$ the zero-sum condition on the second orbit. Writing $Ju = \lambda v$ for such vectors yields the redundant eigenvalues $\lambda_{1,2} = \frac{1}{2}(J_{11} + J_{33} \pm \sqrt{\Delta})$ with $\Delta = (J_{11} - J_{33})^2 + 4J_{31}J_{13}$, where we use indices 1 and 3 to denote a top-predator and its prey, respectively. In the present case redundant eigenvalues can thus form a complex-conjugate eigenvalue pair, potentially leading to oscillatory instabilities.

We emphasize that symmetries present in the steady state do not generally persist when the system departs from this state. Dynamics generated in a symmetric mesoscale motif can therefore spread and impact on the entire network. For instance, in the example discussed above, the oscillatory instability can be inferred solely from analysis of the mesoscale motif, whereas the resulting oscillations may affect the entire network.

In summary, every mesoscale symmetry is associated with one or more dynamical modes that originate from the symmetric motif. If the dynamical modes are stable, then they can be removed from the system without changing the remaining dynamics by replacing each orbit of the symmetry by a single node. For this reduced system, the Jacobian can be obtained according to the rules described in section 3. The reduced Jacobian can, in general, be interpreted as describing a smaller food web, but, potentially with altered parameter values. For the simple cases considered in [30], the parameters of the original predator–prey network and those of the reduced network are related so closely that dynamically equivalent systems could be spotted empirically. However, this is much harder for complicated topologies, such as e.g. in figure 3(d), and for more elaborate models. Even in such complicated cases the aggregated Jacobian can be computed relatively straightforwardly with the procedure proposed here. Notably, the complexity of this reduction increases with the size of the symmetric structure, but is independent of the size of the embedding network.

5. Conclusions

In this paper, we have shown that a previously observed equivalence in the dynamics of food webs [30] is the consequence of localized dynamical modes originating from mesoscale symmetries.

We extended here a recent result [33] to show that certain dynamical modes localize on symmetric structures in food webs. In the cases when such mesoscale structures are present these dynamical modes are independent of the network outside the symmetry. If the localized modes are stable, then aggregating the symmetric structures in a food web as described in section 3 removes them while leaving the remaining dynamics intact, leading to a smaller but dynamically equivalent system.

In principle, the findings of this paper can be used to formulate reduced models for certain food webs. However, requiring exactly identical generalized parameters for symmetric species is a strong restriction when considering real-world food webs. In general, the application to reduce food webs exactly will therefore be of little importance as removing the symmetries leads, at best, to a relatively mild aggregation.
Having said that, the results of this paper should remain approximately valid for situations that are almost symmetric. This may significantly increase the applicability of the present results, especially when taking into account that evolutionary or environmental effects may result in very similar generalized parameters in species holding similar positions in the food web. For instance, well-known allometric scaling laws lead to a similar body mass and metabolic rate in species on the same level of the food web \cite{19, 47, 48}. Additionally, there are certain situations where symmetries arise naturally, for instance in metapopulations where the same species is found in more than one geographical location, or right after speciation events when an ancestral species splits into two newly formed species that are still very similar.

From the point of view of physics, symmetric motifs in networks provide an example of mesoscale structures that have distinct and exact dynamical implications for the dynamics of the network as a whole. The new possibilities opened by this insight are further explored in \cite{49}. Importantly, the implications of mesoscale symmetries can be analysed even in very large networks because computations of the corresponding localized eigenvector and eigenvalue do not require the computation of the complete spectrum of the Jacobian.

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**Appendix A. Reduction of the Jacobian matrix of the competitive-exclusion motif**

In this appendix, we show the explicit reduction of the Jacobian matrix for the competitive-exclusion motif in figure 3(a) in terms of generalized modelling parameters of the model presented in \cite{32, 45}. Furthermore, we show that the reduced Jacobian matrix \( \tilde{J} \) is indeed identical to the Jacobian matrix of the simple predator–prey system in figure 3(b). In terms of generalized modelling parameters, (3) becomes

\[
J = \begin{pmatrix}
\alpha_1 & 0 & 0 \\
0 & \alpha_1 & 0 \\
0 & 0 & \alpha_3
\end{pmatrix}
\begin{pmatrix}
\Psi_1 - \mu_1 & 0 & \gamma_1 \\
0 & \Psi_1 - \mu_1 & \gamma_1 \\
-\frac{1}{2} \Psi_1 & -\frac{1}{2} \Psi_1 & \Phi_3 - \gamma_1
\end{pmatrix},
\]

where \( \alpha_i \) is the biomass turnover rate of species \( i \), \( \Psi_1 \) is the sensitivity of the predation to the abundance of both predators, \( \mu_1 \) is the sensitivity of mortality to the predator abundance of both predators, \( \Phi_3 \) is the sensitivity of primary production to the abundance of prey and \( \gamma_1 \) is the sensitivity of predation for both predators to the abundance of prey. The factors of \( \frac{1}{2} \) in the last row arise because each of species 1 and 2 is responsible for half of the biomass loss of species 3; their effect on species 3 is also weighed by this importance.

Using the results in section 3, the reduced Jacobian matrix (see (4)) is

\[
\tilde{J} = \begin{pmatrix}
\alpha_1 & 0 \\
0 & \alpha_3
\end{pmatrix}
\begin{pmatrix}
\Psi_1 - \mu_1 & \gamma_1 \\
2 \left(-\frac{1}{2} \Psi_1\right) & \Phi_3 - \gamma_1
\end{pmatrix}.
\]

This is identical to the Jacobian matrix for a predator–prey system in which the predator is described by the generalized parameters \( \alpha_1, \Psi_1, \gamma_1, \mu_1 \) and the prey species by \( \Phi_3 \).
Appendix B. Reduction of the Jacobian matrix of the apparent-competition motif

In terms of generalized modelling parameters, the Jacobian matrix in (5) of the apparent-competition motif in figure 3(c) is

\[ J = \begin{pmatrix} \alpha_1 & 0 & 0 \\ 0 & \alpha_2 & 0 \\ 0 & 0 & \alpha_2 \end{pmatrix} \begin{pmatrix} \Psi_1 - \mu_1 & 1 \gamma_1 \\ -\Psi_1 & \Phi_2 - \frac{\gamma_1 + 1}{2} \\ -\Psi_1 & -\frac{\gamma_1 - 1}{2} \end{pmatrix}, \]

where the parameters are the same as those in appendix A. The factors of \( \frac{1}{2} \) in the matrix arise because each of the two prey species is responsible for half of the biomass gain of species 1. In comparison to the Jacobian of the competitive-exclusion motif, the matrix contains the elements \( -\frac{\gamma_1 - 1}{2} \) that couple the symmetric (prey) species. These are the apparent competition terms arising because feeding on one prey species leads to a saturation of the predator that benefits both prey species.

Using the results in section 3, the reduced Jacobian matrix is

\[ \tilde{J} = \begin{pmatrix} \alpha_1 & 0 \\ 0 & \alpha_2 \end{pmatrix} \begin{pmatrix} \Psi_1 - \mu_1 & 1 \gamma_1 \\ -\Psi_1 & \Phi_2 - \frac{1}{2} \gamma_1 \end{pmatrix}. \]

Therefore \( \tilde{J} \) is also identical to the Jacobian matrix of the simple predator–prey system in which the predator is also described by the generalized parameters \( \alpha_1, \Psi_1, \gamma_1, \mu_1 \) and the prey species by \( \Phi_3 \).

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