Received: 12 June 2023 | Revised: 19 June 2024 | Accepted: 1 July 2024

DOI: 10.1111/ele.14484

LETTER

ECOLOGY LETTERS WILEY

# Identifying and explaining resilience in ecological networks

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**Funding information**
Australian Research Council, Grant/Award Number: FT190100645; Securing Antartica's Environmental Future, Grant/Award Number: ARC SRIEAS SAEF SR200100005

**Editor:** Frederick R. Adler

## Abstract

Resilient ecological systems are more likely to persist and function in the Anthropocene. Current methods for estimating an ecosystem's resilience rely on accurately parameterized ecosystem models, which is a significant empirical challenge. In this paper, we adapt tools from biochemical kinetics to identify ecological networks that exhibit 'structural resilience', a strong form of resilience that is solely a property of the network structure and is independent of model parameters. We undertake an exhaustive search for structural resilience across all three-species ecological networks, under a generalized Lotka-Volterra modelling framework. Out of 20,000 possible network structures, approximately 2% display structural resilience. The properties of these networks provide important insights into the mechanisms that could promote resilience in ecosystems, provide new theoretical avenues for qualitative modelling approaches and provide a foundation for identifying robust forms of ecological resilience in large, realistic ecological networks.

KEYWORDS
adaptation, ecosystem, management, resilience, socioecological

## INTRODUCTION

As the Anthropocene drives accelerating global change, resilience is an important and desirable characteristic of ecological systems (Folke et al., 2004). Resilience has a range of definitions, but it generally refers to the capacity of an ecosystem to absorb or withstand perturbations and other stressors, while still maintaining essentially the same function, structure and feedbacks (Carpenter et al., 2001; Holling, 1973; Meyer, 2016; Walker et al., 2004; see Figure 1). Resilient ecosystems do not remain entirely unchanged in the face of perturbations. However, certain critical properties of the system are retained—there could be important ecological processes such as nutrient cycling, or ecosystem services, such as fishery yields (Healey, 2009; Krkošek & Drake, 2014; Waldman et al., 2016).

In conservation and applied ecology, a major hurdle to the application of resilience theory is the need for an accurate quantitative understanding of ecosystem dynamics. A primary approach to measuring the resilience of an ecological system is to create and parameterize a dynamical model of the system and then to simulate its response to perturbations (Carpenter et al., 2001; Meyer, 2016; Mumby et al., 2014; Urruty et al., 2016). However, the complexity of ecological systems, paired with sparse, noisy data sets, make this parameter estimation process very challenging (Adams et al., 2020; Botelho et al., 2024; Carpenter et al., 2005; Meyer, 2016; Remien et al., 2021).

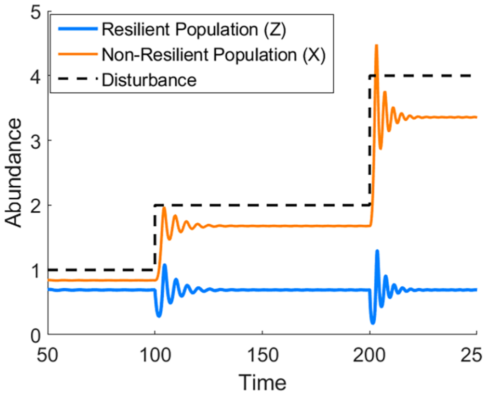


**FIGURE 1** In this example of *structural resilience*, or *robust perfect adaptation*, the abundance of species $Z$ returns precisely to its original abundance despite a persistent press perturbation. Species $Z$ can exhibit structural resilience because species $X$ absorbs the effects of the perturbations and does not return to its original abundance. This ecosystem is shown in Figure 3e. Full details on the model equations, parameters and initial conditions are given in Supporting Information.

Resilience would be easier to identify and operationalize if it were a structural property of the ecosystem—that is, a consequence of the shape of the ecological network, rather than the strengths of all the interactions. Indeed, the search for ecosystem structures that could robustly deliver resilience was an early motivation for qualitative modelling (Bode et al., 2017; Dambacher et al., 2003; Levins, 1974; Raymond et al., 2011). The existence of such 'structural resilience' would effectively side-step the empirical challenges of estimating the parameters of ecosystem models. It is much easier to identify that a particular species interaction is competitive, for example, than it is to estimate the per-capita strength of that competition (Adams et al., 2020; Botelho et al., 2024). Studies into resilience of socioecological systems have also proposed that certain networks structures—'motifs'—can support resilience (Barnes et al., 2017; Janssen et al., 2006). However, this research is phenomenological: a small number of resilient network motifs are proposed, primarily on the basis of intuition, and their association with resilient dynamics is assessed statistically. This limits the insights that these methods can offer to other systems and the generality of their conclusions.

Within living organisms, biochemical reaction networks can exhibit 'robust perfect adaptation' (RPA), a phenomenon that is closely analogous to structural resilience (Alon et al., 1999; Araujo & Liotta, 2023a; Kaupp, 2010; Ma et al., 2009). In RPA networks, a subset of chemical species are able to precisely maintain or recover their abundances following press or pulse perturbations (Araujo & Liotta, 2018; Ma et al., 2009). RPA is an important and common property of cellular systems, despite external perturbations. It has been observed in systems scaling from chemotaxis within single-celled organisms (Alon et al., 1999; Kollmann et al., 2005; Levchenko & Iglesias, 2002; Macnab & Koshland Jr, 1972; Parent & Devreotes, 1999; Yi et al., 2000) through to complex sensory systems such as our sense of smell (Kaupp, 2010; Matthews & Reisert, 2003; Reisert & Matthews, 2001; Yau & Hardie, 2009). In a sense, the whole biochemical reaction network can be understood as a perturbation-absorbing mechanism which ensures that key outputs are maintained at a consistent level (Araujo & Liotta, 2018, 2023a, 2023b; Ma et al., 2009; see Figure 1).

Crucially, RPA is solely a property of the structure of the biochemical reaction network (Araujo & Liotta, 2018, 2023b). Identifying robust perfect adaptation therefore does not require precise knowledge of the parameter values of the network model, a fact that is both conceptually interesting and practically important in biochemistry and ecology. (Hereafter, to avoid interdisciplinary confusion, we will eschew the term adaptation and refer only to structural resilience. This is because in ecology and evolution, adaptation refers to changes to the structure of the network itself, rather than the recovery of the system state. Meanwhile, in socioecological resilience theory 'adaptability' refers to the changing behaviour of actors in the system (Barnes et al., 2017; Walker et al., 2004)).

If structural resilience could be found in the dynamics of ecological networks, it would represent a strong but narrow form of resilience. In an ecosystem with structural resilience, the populations of a subset of species would return to their exact pre-perturbation abundances, despite continuing press perturbations. Any ecosystem functions, services or identity that depended primarily on those species would therefore be resilient to the perturbation. Moreover, an observer would be able to predict this behaviour on the basis of the network structure alone, even if they were unable to measure the strengths of the interactions between the species. However, the remaining species in the system would not return to their pre-perturbation abundances. They could not, since it would be these species that were together absorbing the effects of the perturbation. The ecosystem would therefore not be resilient if its important properties were a function of the abundance of these species.

In this study, we introduce a set of analytical tools from biochemical reaction network theory to search for the presence of structural resilience in the dynamics of ecological networks. We start by describing an algebraic approach for identifying structural resilience and multiple attractors in ecosystem dynamics. Then, we undertake an exhaustive computational search through all possible three-species ecosystems under the generalized Lotka-Volterra equations—a commonly used modelling framework in ecology. Third, we identify what properties of the ecosystem network structure are required to exhibit structural resilience. Finally, we consider how an understanding of structural resilience could be utilized to pursue practical conservation outcomes.

# METHODS

In this section, we introduce the algebraic methods that are capable of identifying structural resilience and describe how we set up an exhaustive search through all possible three-node species interaction networks. Although we will generally refer to them as species, each node could also represent the combined populations of similar species (e.g., a functional group or guild (Peterson et al., 2021; Zheng et al., 1997)). We model these ecosystems using generalized Lotka-Volterra equations, but the methods described in this paper could be applied to other functional forms such as Holling-type interactions or Rosenzweig-MacArthur models. Similarly, we apply press perturbations to the species, but press perturbations could be applied to the interactions in the network. To accompany the following discussion, we provide a worked example in Supplementary Methods S2 and a coded example at https://zenodo.org/records/12026654 (Jeynes-Smith, 2024; along with all code developed for this study). This coded example can be altered to search for structural resilience in networks that have more nodes or using models with different functional forms.

## Network models

For each interaction network, we check that the abundance of at least one species can be maintained in the face of a perturbation that affects one or more of the species. We identify this as the network 'output', $Z$. However, we will later assess whether the other species, labelled as $X$ and $Y$, are also able to maintain their abundance in the face of the perturbation.

We are primarily interested in structural resilience to a persistent press perturbation. We consider perturbations that impact one or more of the species in the network. This could represent the effects of persistent human activity that targets a single species, such as fishing or hunting, or conservation management actions such as invasive species control or supplementary feeding. It could also represent management that would affect multiple species or the whole ecosystem, such as habitat degradation or a long-term change in climatic conditions. We do not investigate pulse perturbations, such as a single culling event or species translocation, nor do we consider perturbations that alter the types of interactions between the species.

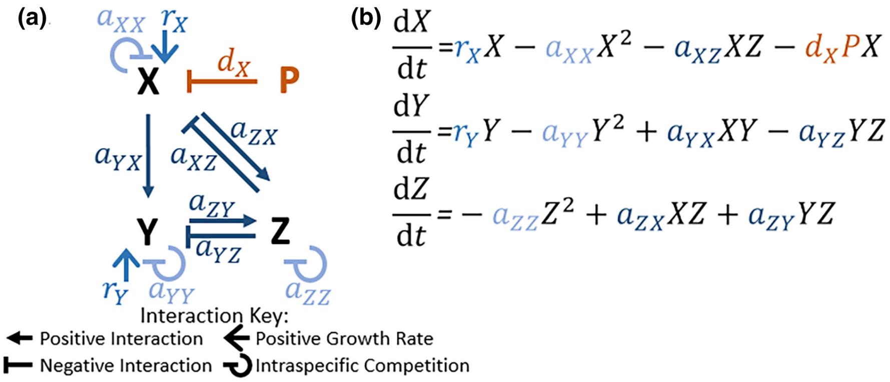
In their general form, the Lotka-Volterra equations (Bode et al., 2017; Lotka, 1925; Volterra, 1926) describe the dynamics of the ecosystem as:

$$\frac{dX}{dt} = \overbrace{r_X X}^{\substack{\text{Intrinsic}\\ \text{Growth}}} - \overbrace{a_{XX}X^2}^{\substack{\text{Intraspecific}\\ \text{Competition}}} + \overbrace{a_{XY}XY + a_{XZ}XZ}^{\substack{\text{Interspecific}\\ \text{Interactions}}} + \overbrace{d_X PX}^{\text{Perturbation}}, \tag{1}$$

$$\frac{dY}{dt} = r_Y Y - a_{YY}Y^2 + a_{YX}XY + a_{YZ}YZ + d_Y PY, \tag{2}$$

$$\frac{dZ}{dt} = r_Z Z - a_{ZZ}Z^2 + a_{ZX}XZ + a_{ZY}YZ + d_Z PZ, \tag{3}$$

where $X$, $Y$, and $Z$ are the abundances of the interacting species (see Figure 2a); $r_i$ is the intrinsic growth rate of species $i$; $a_{ij}$ is the (*per-capita*) interaction constant for how species $i$ is affected by species $j$; and $d_i$ is the interaction constant for how the perturbation, $P$, affects species $i$. It is by systematically adding and removing combinations of these terms that we are able to test for the existence of structural resilience in all possible networks.



$$\frac{dX}{dt} = r_X X - a_{XX}X^2 - a_{XZ}XZ - d_X PX$$
$$\frac{dY}{dt} = r_Y Y - a_{YY}Y^2 + a_{YX}XY - a_{YZ}YZ$$
$$\frac{dZ}{dt} = -a_{ZZ}Z^2 + a_{ZX}XZ + a_{ZY}YZ$$

FIGURE 2 (a) Graphical representation of ecosystem with three species, $X$, $Y$, and $Z$, and perturbation $P$. In this ecosystem, $Z$ predates on both $X$ and $Y$, and $X$ positively affects $Y$ without being affected itself. Species $X$ is affected by the perturbation. Parameters are coloured by type: Intraspecific competition (light blue), intrinsic growth rates (blue), interspecific interactions (dark blue) and press perturbations (orange). (b) Associated generalized Lotka-Volterra equations.

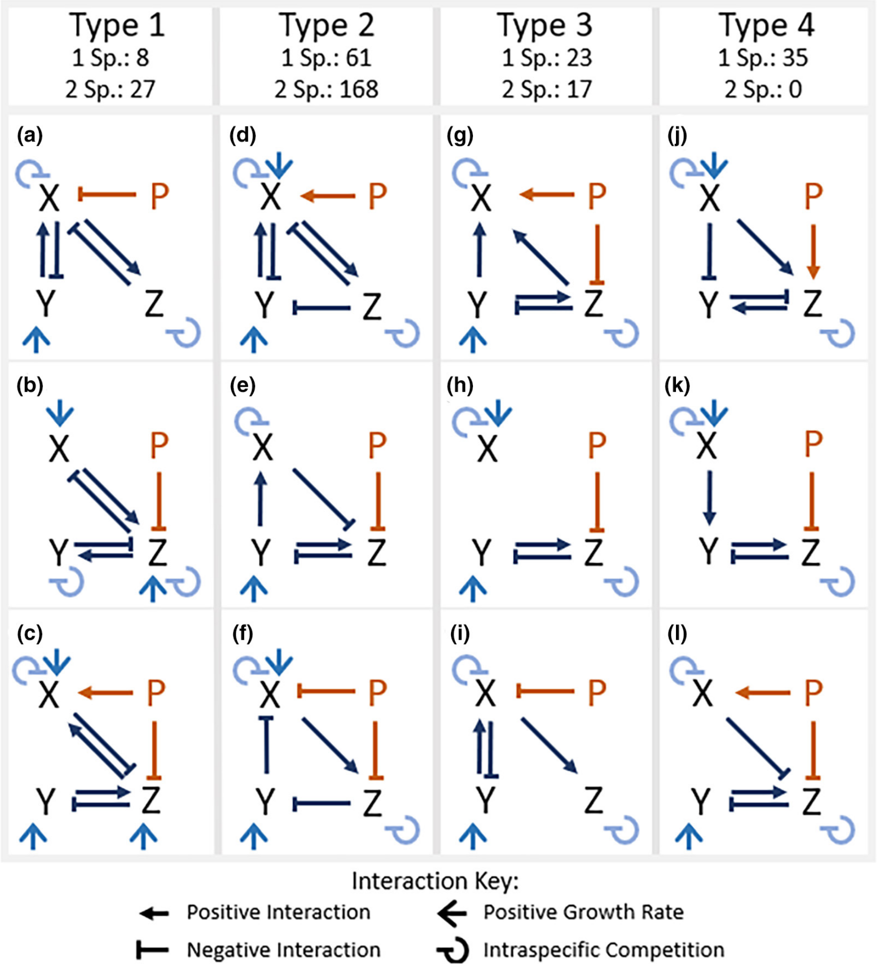


**FIGURE 3** Four motifs that produce structural resilience, with three example species interaction networks for each type. Motifs are differentiated by (i) the underlying mechanism that enables structural resilience and (ii) how that mechanism interacts with the ecosystem. The interaction signs permit stable, feasible steady states. For each type, we specify the number of motifs which had one species (1 Sp.) and two species (2 Sp.) with structural resilience.

Lotka-Volterra equations describe the net effect of *direct* interactions between species using the interspecific interaction parameters, $a_{ij}$: indirect interactions arise implicitly (e.g., apparent competition). As an example of a direct interaction, Figure 2 includes a predator–prey interaction between $Y$ and $Z$. The predator, $Z$, will increase in abundance (positive value of $a_{ZY}$) proportional to the abundance of predators and the prey, $Y$, which are available to consume; the prey abundance declines too, but according to the rate $a_{YZ}$. Note, that $Z$ also indirectly negatively interacts with $Y$ via its consumption of $X$, a species which provides a benefit to $Y$.

Interactions are not limited to predator–prey relationships. The signs of symmetric coefficient pairs, $\left(a_{ij}, a_{ji}\right)$, characterize each interspecific interaction. Some common examples include: competition, $a_{ij}, a_{ji} < 0$; mutualism, $a_{ij}, a_{ji} > 0$; and predator–prey, $a_{ij} > 0$, $a_{ji} < 0$ where population $i$ is the predator. Such two-way interactions are visually represented in a network diagram by a pair of arrows (e.g., the predator–prey interaction between $Y$ and $Z$ in Figure 2). We also allow for one-way interactions, represented with a single arrow, where only one species is affected by the interaction either amensal, $a_{ij} = 0, a_{ji} \neq 0$; or commensal $a_{ij} \neq 0, a_{ji} = 0$. For example, $Y$ could be said to have a commensal one-way interaction, where it benefits from the presence of $X$, in Figure 2. One-way interactions occur in nature (Abrams, 1987), such as ecosystem engineering or allelopathy, but are thought to be less common than two-way interactions (Dittmann, 1990; Gómez-Aparicio & Canham, 2008; Hulme-Beaman et al., 2016; Mathis & Bronstein, 2020; Peterson et al., 2021; Rasmussen & Rasmussen, 2018).

The other two key terms in our models are each species' intrinsic growth rates, $r_i$, and intraspecific competition terms, $a_{ii}$. The intrinsic growth term represents positive influences on the growth rate of population $i$ which are not explicitly included in the network (Barbier & Loreau, 2019; Bode et al., 2017; O'Dwyer, 2018; Peterson et al., 2021). These terms are often included for lower trophic-level species such as vegetation, where the sources of growth like nutrient are modelled implicitly. Intraspecific competition, also referred to as self-regulation, occurs where processes such as competition for the same resources, such as habitat, will ultimately limit a species ability to increase in abundance (Anisiu, 2014; Barbier & Loreau, 2019; Bode et al., 2017; Hening & Nguyen, 2018; O'Dwyer, 2018; Peterson et al., 2021; Wangersky, 1978). We considered networks where these terms were both included and excluded for each species. Networks where some species do not have these terms can still describe feasible ecosystems (i.e., where all species can persist). Species without an intrinsic growth term can increase by consuming other species in the network (Barbier & Loreau, 2019; Peterson et al., 2021); species without an explicit intraspecific competition term can reach stable abundances through the limited availability of prey species, or because they are controlled by predation (Barbier & Loreau, 2019; Lotka, 1925; O'Dwyer, 2018; Volterra, 1926). Ecosystem models that do not include both these terms for every species in the model are less common in the literature; however, because they are ecologically plausible, we include them in our exhaustive search.

We illustrate a graphical representation of a network and the associated Lotka-Volterra equations in Figure 2.

## Identifying the capacity for structural resilience

We adapt analytical methods developed by Araujo and Liotta (Araujo & Liotta, 2023b) to identify structural resilience in ecological systems. These methods can identify the capacity for structurally resilient networks on the basis of their structure alone, regardless of the precise strength of these interactions.

We use a full factorial design to enumerate every possible combination of the terms in Equations (1)–(3). There are a total of $5 \times 2^{12} = 20{,}480$ possible network structures (not considering the sign of the interactions), since there are 12 parameters and five unique combinations for how the perturbation affects subsets of the species: (i) $X$, (ii) $Z$, (iii) $X$ and $Y$, (iv) $X$ and $Z$ and (v) all three species. Note that species $X$ and $Y$ are interchangeable which reduces the number of unique combinations in which the perturbation interacts with the network. Given this large number of potential models, efficient methods are needed to exhaustively test for the structural resilience property.

The core of this approach is the realization that any network with structural resilience must have a steady-state solution in which the abundance of at least one species is independent of the perturbation variable (Araujo & Liotta, 2023b). We use methods from algebraic geometry, specifically Gröbner bases, to determine whether the system's 'governing equations' (in this case the generalized Lotka-Volterra equations) can be algebraically transformed (projected) into the following form:

$$p_1 \frac{dX}{dt} + p_2 \frac{dY}{dt} + p_3 \frac{dZ}{dt} = f(P, Z)(Z - k). \tag{4}$$

Here $p_1, \ p_2, \ p_3$ are polynomials in the network variables (e.g., $Z, Y, X$), $dX/dt, \ dY/dt, \ dZ/dt$ are the governing equations (e.g., Equations (1)–(3)), $f(P, Z)$ is a polynomial in the perturbation $P$ and target species $Z$, and $k$ is a constant (a function of the network parameters). The right-hand side of Equation (4) is referred to as an RPA polynomial (see (Araujo & Liotta, 2023b)). Importantly, at steady-state ($dX/dt = dY/dt = dZ/dt = 0$), a solution for this system will always be $Z = k$, which is independent of any change to the perturbation, $P$, and all other variables in the network ($X$ and $Y$). This particular solution, $Z = k$, is referred to as the setpoint and identifies the abundance which the target should return to after any disturbance. Importantly $f(P, Z)$ can be used to identify all alternative steady states for species $Z$ (Araujo & Liotta, 2023b). If this polynomial has several real, stable solutions, then the system may only display structural resilience for a limited set of perturbation strengths (Araujo & Liotta, 2018, 2023b).

To find a solution for species $Z$ relative to $P$, it is possible to manually manipulate the governing equations of a network at steady state. For example, consider the following system of Lotka-Volterra equations:

$$\frac{dX}{dt} = -a_{XX}X^2 + a_{XZ}XZ$$
$$\frac{dY}{dt} = r_Y Y - a_{YX}XY$$
$$\frac{dZ}{dt} = -a_{ZX}XZ + a_{ZY}YZ - d_Z PZ$$

Under the assumption that the equations are at steady state and that the abundances are nonzero, we can simplify these equations to be,

$$0 = -a_{XX}X + a_{XZ}Z, \tag{5}$$

$$0 = r_Y - a_{YX}X, \tag{6}$$

$$0 = -a_{ZX}X + a_{ZY}Y - d_Z P. \tag{7}$$

We can rearrange Equation (6) to obtain $X = \frac{r_Y}{a_{YX}}$ and substitute this result into Equation (5) to obtain an expression for $Z$,

$$Z = \frac{r_Y a_{XX}}{a_{YX} a_{XZ}}.$$

Since this solution for $Z$ is independent of the perturbation, $P$, and the other variables, $X$ and $Y$, the network is declared to have the capacity for structural resilience. This assumes that all species remain extant and that the solution is stable. Importantly, altering the sign or strength of the parameters in this solution will not change the existence of this solution—a result which held true for all networks that we examined. This demonstrates how the presence of structural resilience is independent of the sign and strength of parameters (Araujo & Liotta, 2018). However, as we discuss shortly, the sign and strength of parameters do play an important role in determining whether the setpoint, and other solutions of $f(P, Z)$, are feasible and stable. We include several worked examples of this manual approach in Supplementary Methods S1.

This manual process of manipulating equations can be applied to individual networks, however applying this to a large number of networks is inefficient. Gröbner bases allow the manipulation process to be automated, without making any assumptions about species' abundances (Araujo & Liotta, 2023b). A Gröbner basis is effectively an alternate presentation of the governing equations, which captures all steady states in a form that reveals the most relevant steady state properties. In this case, we seek to match all steady state solutions for $Z$ to the RPA polynomial and identify steady states independent of the perturbation (Araujo & Liotta, 2023b). For this, we compute a Gröbner basis with an 'elimination ordering' where the governing equations can be rewritten with respect to a decreasing number of variables, based on a specified order. To identify an RPA polynomial we choose an order in which the target species, $Z$, and the perturbation, $P$, should be the last variables in the set of equations. When we compute a Gröbner basis, we confirm the existence of functions $p_1$, $p_2$ and $p_3$ in Equation (4), which transform the governing equations into the RPA polynomial. A network does not have structural resilience if the solutions do not only contain the two variables $P$ and $Z$, or for which the solutions cannot be factorized into an RPA polynomial. For an in-depth explanation of the underlying mathematics of the RPA polynomial and the implementation of Gröbner bases, see (Araujo & Liotta, 2023b). We use Matlab's (The MathWorks Inc, 2019) symbolic toolkit to automate the calculation of Gröbner bases and determine whether the solutions can be factorized into an RPA polynomial.

For the above example, an associated Gröbner basis is given by,

$$p_1 \frac{dX}{dt} + p_2 \frac{dY}{dt} + p_3 \frac{dZ}{dt} = r_Y d_Z Z P \left(a_{XZ} a_{ZX} Z + a_{XX} d_Z P\right)\left(Z - \frac{r_Y a_{XX}}{a_{YX} a_{XZ}}\right).$$

From this, we can identify the same setpoint that we had manually, $Z = \frac{r_Y a_{XX}}{a_{YX} a_{XZ}}$, but also the other solutions to $Z$ in $f(P, Z) = r_Y d_Z Z P \left(a_{XZ} a_{ZX} Z + a_{XX} d_Z P\right)$. We assume that there is a persistent perturbation, $P > 0$. If $Z$ remains extant, $Z > 0$, then the only feasible solution is when $Z$ is at the setpoint.

Although they can require significant time and memory to compute for large or highly connected networks (Araujo & Liotta, 2023b), Gröbner bases may be calculated for any modelling equations consisting only of polynomial functions of the model variables. This fact makes them suitable for the study of many modelling frameworks. In addition to the Lotka-Volterra equations, other common modelling frameworks, such as Holling-type reactions or Rosenzweig-MacArthur models, can also be written as polynomials when at steady state.

Structural resilience requires the existence of an RPA polynomial, however we must still determine whether the setpoint, $Z = k$, is a feasible and stable steady state (Araujo & Liotta, 2023b). Feasibility ensures that all species have a positive abundance at steady state, while stability ensures that our ecosystem can approach that steady state. In nature, any observed ecosystem is likely to be both feasible and stable (it would not exist without these properties), but in our exhaustive search we do not want to consider species interaction networks that cannot stably exist.

Since the projection test significantly reduces the number of networks (20,480 to 3142 networks, see Supplementary Figure S1), we test for stability and feasibility using $4 \times 10^3$ randomly selected parameter sets for each network. Note that since structural resilience should be independent of fine-tuning parameters, we do not require an extensive search of parameter space. Parameters are selected from uniform distributions, $x \in (-1, 1)$ for interspecific or perturbation interaction parameters, $x \in (0, 1)$ for intrinsic growth rates, and $x \in (-1, 0)$ for intraspecific competition parameters. Any Lotka-Volterra system can be rescaled to have coefficients within these bounds without loss of generality (Bode et al., 2017). We calculate the steady states of a network, match these to the setpoint, then substitute in random parameter values and check for feasibility for all species. If the steady state is feasible, then we check for Lyaponuv stability (Lyapunov, 1992). If both stability and feasibility conditions are met for any parameter set, then the network is capable of structural resilience.

We lastly ensure that successful networks have structural resilience and not a trivial form in which the output species has no reaction to a change in perturbation (Ma et al., 2009). We simulate each network, using Matlab's (The MathWorks Inc, 2019) 'ode45' adaptive solver, and check that the output reacts to a change in perturbation by at least 1% of its pre-perturbation abundance and then returns to within 1% of its pre-perturbation abundance for two perturbations which double in strength ($P \in \{1,2,4\}$) every 1000 time steps. This simulation test will reject networks which are readily absorbed by alternate attractors for a set of perturbation strengths. For networks which pass all of the above tests, we generate 2000 parameter sets that enable feasible and stable steady states, and use these for further analysis. See Figure S1 for a graphical representation of this process and the number of networks which proceed after each test.

## RESULTS AND DISCUSSION

In the following sections, we classify the ecosystem networks that exhibited structural resilience. We then identify and explain the specific network structures which enable a subset of the species maintain their abundance in the face of a persistent press perturbation. We discuss how these characteristics, and the associated transient dynamics, affect the possibility of observing structural resilience in realistic ecosystems. Lastly, we discuss how an understanding of structurally resilient networks could be used in a conservation context.

## Network structures with structural resilience

A total of 339 networks exhibit structural resilience for at least one of the three species. Of these, most (212, $\sim 63\%$) exhibit structural resilience for two of the three species (see Figure S2 for example). We categorize these networks into four motifs based on the specific combination of interspecific interactions that enable structural resilience. Figure 3 shows three examples of each type of network. The full list of 339 networks (without assigned sign structure) can be found in Figure S3.

The first structurally resilient motif consists of two predator–prey reactions across three trophic levels (Figure 3a–c). This motif achieves structural resilience via a species at the bottom of the food chain which absorbs the perturbation. This motif was present in 35 networks, of which 77% exhibited structural resilience for a second species.

The second structurally resilient motif uses a feedback loop to maintain species abundances, where a change in the abundance of $Z$ loops back through the network to $Z$ (Figure 3d–f). Here, species are connected by one (Figure 3d), two (Figure 3e), or three (Figure 3f) one-way interactions. At least one of these interactions must be one-directional to enforce a direction on the feedback loop. This is the most common motif, with 229 networks, of which 168 (73%) have structural resilience for two of the three species.

The third and fourth structurally resilient motifs are dependent on a single 'predator–prey' interaction, with a third species that either does not contribute to the mechanism (motif 3 in Figure 3g–i), or contributes as a 'regulating' species (motif 4 in Figure 3j–l). In Type III motifs, the single predator–prey reaction between $Z$ and an intermediate species enables structural resilience. Additional one-way interactions from the predator and prey can 'regulate' the third without it influencing their abundances. In Figure 3i, there is a notable distinction where the predator–prey interaction occurs between $X$ and $Y$. In this network, species $X$ has structural resilience, and confers the property to species $Z$ via the one-way interaction (see Figure S2). Motif 3 was represented by 40 structurally resilient networks, of which only 43% had structural resilience for a second species.

In Type IV motifs, the species outside of the predator–prey interaction influences the abundance of the predator and/or prey, via one-way interactions. The third species is effectively isolated and will never have structural resilience: It either never reacts to a change in perturbation (Figure 3j,k), or its abundance always changes with the perturbation (Figure 3l). The intermediary species—which participates in the predator–prey interaction with $Z$—always changes following a perturbation, since it must absorb changes to enable structural resilience in $Z$. As a consequence, in networks that follow Type IV motifs, only one species exhibits structural resilience.

We examine all five ways in which the perturbation can affect the network (excluding the sign and strength of those interactions): (i) $X$; (ii) $Z$; (iii) $X$ and $Y$; (iv) $X$ and $Z$; (v) and $X$, $Y$, and $Z$. Only three of these combinations have networks capable of structural resilience: $X$, $Z$ or $X$ and $Z$. Structural resilience cannot be found when the perturbation impacts $X$ and $Y$, or impacts all three species. This result implies that structural resilience cannot occur when a perturbation directly affects all species in the network, as it might for climatic perturbations such as climate change. This mirrors results from biochemical kinetics, where networks of any size cannot exhibit robust perfect adaptation when all components are simultaneously perturbed (Araujo & Liotta, 2023a, 2023b).

Structurally resilient motifs have some ecologically unusual properties. All four motifs contain species with intrinsic growth and self-regulation terms, but none include these terms for all three species. Many of the 339 networks that are capable of structural resilience are dependent on one-way interactions (Figure 3d–l), although not networks with the Type I motif. A few contain multiple one-way interactions in sequence (Figure 3e,f).

## Large oscillations and transient dynamic limitations

Generalized Lotka-Volterra models often generate oscillatory transient dynamics (Anisiu, 2014; Wangersky, 1978), and the networks which we identify as having structural resilience also display this behaviour (Figure 4a). When impacted by a perturbation, some of our networks quickly asymptote to their equilibrium, but others rapidly oscillate in response, sometimes cycling hundreds of times before returning to the setpoint (Figure 4a). If another perturbation occurs within this oscillatory period it is possible that a species can be perturbed to extinction, despite the network having the structural resilience property (Figure 4b). Studies of classical resilience often focus on how networks can be parametrically changed to reduce these oscillations, where one possible requirement is to enforce strong self-regulation terms (relative to the other interactions in the network) for more species (Anisiu, 2014; Carpenter et al., 2001; Hening & Nguyen, 2018; Holling, 1973; Lavorel, 1999; Meyer, 2016; Neubert & Caswell, 1997; Wangersky, 1978).

The oscillatory behaviour is related to the particular mechanism that generates the structural resilience property. In biochemical networks, two overarching

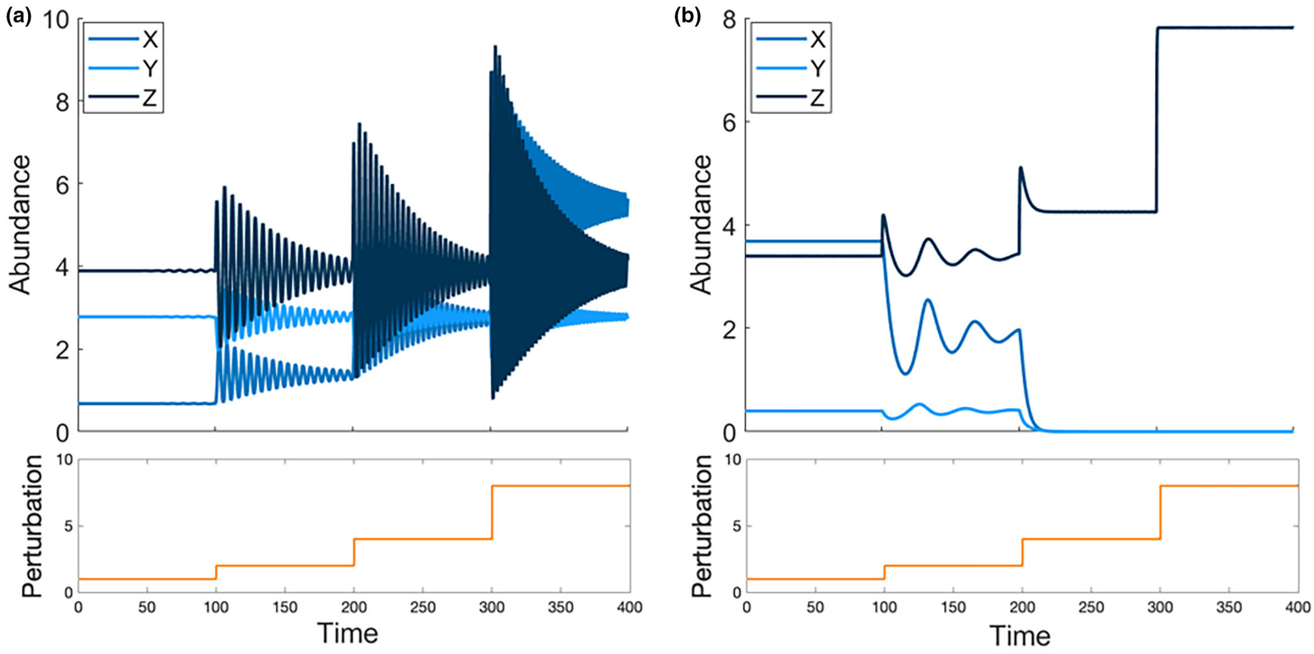


**FIGURE 4** Two examples of oscillating behaviour in structurally resilient ecosystems following press perturbations. (a) highly oscillatory response to perturbations, where increasing press perturbations increase the frequency and amplitude. (b) increasing press perturbations drive a species to extinction, even for ecosystems with structural resilience. Full details on the model equations, parameters and initial conditions are given in Supporting Information.

mechanisms have been identified as responsible for robust perfect adaptation (i.e., structural resilience): Balancer and Opposer mechanisms (Araujo & Liotta, 2018, 2023a, 2023b). Balancer mechanisms require multiple 'paths' which connect the perturbed species to the output species, where a path is a sequence of species interactions. These paths contain 'computational' species which effectively 'balance out' changes caused by the perturbation. Importantly, for these paths to exist, the perturbed species and output must be different species. An example of this structure is predator-mediated competition where one 'path' is the direct effect between the predator and prey species, and a second 'path' utilizes the indirect effect of the predator via its consumption of the species which competes with the prey (Chase et al., 2002). Opposer mechanisms utilize a different class of 'computational' species, embedded within a feedback loop, that negates the effects of the perturbation. The feedback loop is a sequence of species interactions which connects the output species to itself, via other species. Unlike Balancer mechanisms, the perturbed species and output species can be one and the same in Opposer mechanisms. Because these two mechanisms depend on the dynamics of the 'computational' species, the choice of modelling framework can alter which networks meet the requirements of the 'computational' species and display structural resilience.

All of the structurally resilient networks utilize Opposer mechanisms. In many of our structurally resilient networks, the perturbation directly affects species $Z$. The perturbed species and output species is therefore the same, and these networks must utilize Opposer mechanisms. In those networks where only $X$ is affected by the perturbation, we do not observe multiple 'paths' because of the presence of one-way interactions. Importantly, Opposers are known to create oscillatory behaviours because of the feedback structure (Araujo & Liotta, 2023a).

## Implementation and applications

Mathematical modelling provides an opportunity for testing conservation actions at low cost and without risk. In this section, we demonstrate how structural resilience could be identified and used in a conservation context. In Figure 5, we propose a coexisting four-species ecosystem consisting of a species of conservation value, $Z$, and a pest species, $W$. At time $t_1$, a persistent press perturbation $P$ , such as an increase in specific human land-use, results in the valuable species decreasing to extinction (Figure 5 dashed line). Our methods identify that without the presence of the pest, $W$, our network exhibits structural resilience for species $Z$ (Figure 3e). At $t_2$ we therefore eradicate the pest species and observe that the valuable species is not only able to recover from the initial perturbation and persist, but it is able to recover its abundance following an increase in the perturbation at $t_3$.

We have only examined small ecosystem networks in this work to allow for an exhaustive search of all structures. However, the methods which we have demonstrated can be applied to larger species interaction networks, alternate modelling frameworks, and different perturbations.

The smaller networks which we have identified as being capable of structural resilience can also be modified, or they can be viewed as components of larger networks without the loss of structural resilience. Araujo and Liotta have defined several guiding principles for embedding or manipulating networks (Araujo & Liotta, 2018, 2023a, 2023b), but generally, additional interactions must maintain the functionality of the specific mechanism which enables structural resilience in the network.

In Figure 6, we demonstrate how the ecosystem in Figure 3e (Network A) can be altered to include extra interactions and species. The mechanism which enables structural resilience in this network is the feedback loop which follows the path $Z \rightarrow Y \rightarrow X \rightarrow Z$, where $Y$ is the computational species which absorbs the change in perturbation, maintaining the abundance of $Z$. When including new interactions, structural resilience will not be affected if we do not alter the direction of the feedback loop or directly affect $Y$. In Network B, we demonstrate how another species can be included along the feedback loop without losing the structural resilience property. We are also able to introduce interactions between $X$ and $Z$, or self-regulation terms on $Z$ without losing the structural resilience property (Figure 6, Network C). In fact, by including self-regulation for $Z$, we are able to dampen the oscillations. However, by including interactions that directly affect $Y$, we alter the structural resilience mechanism and lose the property (Figure 6 Network D). Alterations such as these could be applied on a much larger scale to identify new networks. Networks can also become larger if individual nodes become more complex. For example, Figure S4 demonstrates how additional nodes that introduce size or age structure into the ecosystem model do not affect its structural resilience.

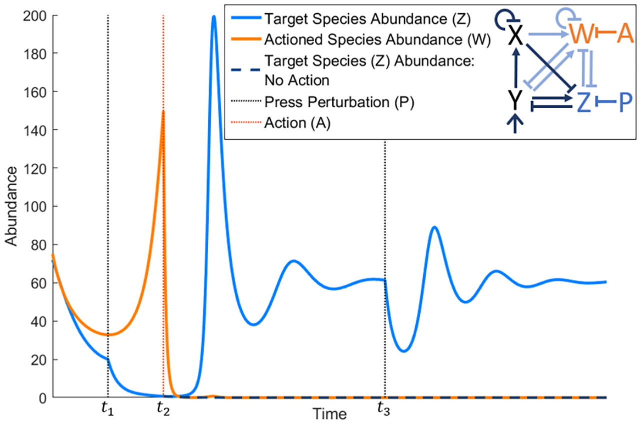


**FIGURE 5** Demonstration of how a conservation action can save a species from extinction by creating structural resilience. The full network (top right) is feasible and stable and contains four coexisting species. However, the ecosystem is not structurally resilient, and so a press perturbation (black dotted line) drives the target species to extinction. However, removing species $W$ and its network interactions (light blue in diagram) via a targeted press perturbation (action—red dotted line), creates structural resilience for $Z$ in the remaining ecosystem (see Figure 3e). Species $Z$ is thereafter able to persist, even in the face of a stronger press perturbation. Full details on the model equations, parameters and initial conditions are given in Supporting Information.

## CONCLUSION

In this study, we interpreted methods from biochemical kinetics to the context of ecological resilience theory. We focused on structural resilience—the ability of a subset of species within an ecosystem to perfectly return to their original, pre-perturbation abundances. Structural resilience is a strong but narrow subset of traditional resilience: It only applies to some of the components of the ecosystem, but it also applies to any ecosystem with that structure, independent of the strength of its parameters. This decreases the reliance on data to predict resilience

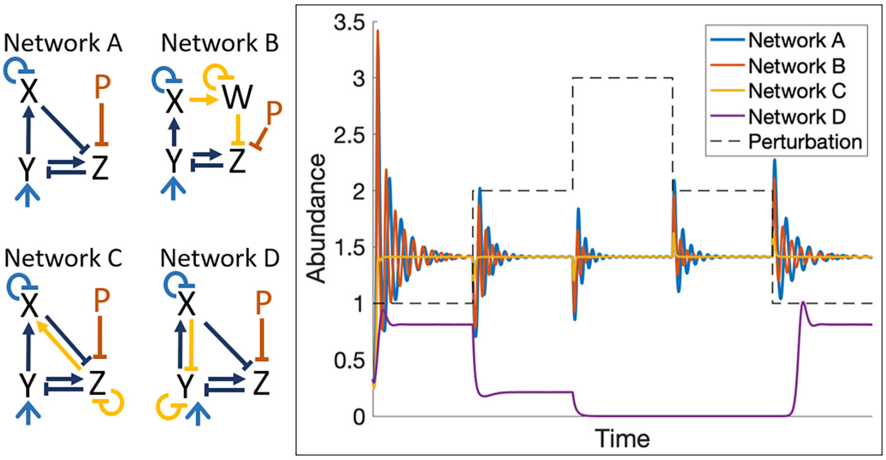


**FIGURE 6** Simulated abundance of a target species, $Z$, to press perturbations, in a range of modified networks. Network A is a known structurally resilient network from Figure 3e. In Network B–D, small alterations are made to the network as indicated by the yellow arrows. When adding interactions that do not directly alter the mechanism which enables structural resilience (Networks B, and C), then structural resilience can still be obtained, but if the mechanism is altered (Network D), then structural resilience is lost (purple line). Full details on the model equations, parameters and initial conditions are given in Supporting Information.

and can utilize expert knowledge about interactions between species (Adams et al., 2020; Botelho et al., 2024; Peterson et al., 2021; Remien et al., 2021).

We identified 339 three-species networks under the generalized Lotka-Volterra equations which were capable of structural resilience, most of which displayed the property for two of three species. Of these structurally resilient networks, our Type I networks resembled realistic hierarchical structures of predation across multiple trophic levels (Dunn et al., 2017; Kar et al., 2019; Lewis et al., 2014; Salomon et al., 2010). For the majority of networks, we observed several features which seemed ecologically unusual, including the presence of one-way interactions sequences, the absence of some intrinsic growth and self-regulation terms and oscillatory behaviours.

Despite the small number of structurally resilient networks which we have identified, there are a multitude of alterations, such as larger networks, alternate modelling frameworks and perturbations, and age/size-structured behaviours, which we can test with these methods. This study presents an introduction to structural resilience in ecological networks and proves that the property may be found in ecosystems. In 2009, a study by Ma et al. (2009). which exhaustively identified resilience in biochemical reactions with three components provided critical insights into the phenomenon that led to a full understanding of the constraints and mechanisms that enable structural resilience in any-sized biochemical network (Araujo & Liotta, 2018, 2023a, 2023b). This study offers the same initial stepping stone, opening the door for more analytical studies in ecological systems.

## AUTHOR CONTRIBUTIONS

CJS conceptualized the idea, RPA contributed to the modelling framework, CJS implemented methods, analysed results, created visualizations and produced the first draft of the manuscript. All authors contributed to the review and editing of the manuscript, and MB and RPA supervised the project.

## ACKNOWLEDGEMENTS

Computational resources and services used in this work were provided by the eResearch Office, Queensland University of Technology, Brisbane, Australia. Open access publishing facilitated by Queensland University of Technology, as part of the Wiley - Queensland University of Technology agreement via the Council of Australian University Librarians.

## FUNDING INFORMATION

Australian Research Council, Grant/Award Number: FT190100645; Securing Antartica's Environmental Future, Grant/Award Number: ARC SRIEAS SAEF SR200100005.

## CONFLICT OF INTEREST STATEMENT

We declare that we have no competing interests.

## PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14484.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://zenodo.org/records/12026654.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Jeynes-Smith, C., Bode, M. & Araujo, R.P. (2024) Identifying and explaining resilience in ecological networks. *Ecology Letters*, 27, e14484. Available from: https://doi.org/10.1111/ele.14484