The role of predator overlap in the robustness and extinction of a four species predator–prey network

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A R T I C L E   I N F O

A B S T R A C T

Predators and preys often form species networks with asymmetric patterns of interaction. We study the dynamics of a four species network consisting of two weakly connected predator–prey pairs. We focus our analysis on the effects of the cross interaction between the predator of the first pair and the prey of the second pair. This is an example where the predator overlap, which is the proportion of predators that a given prey shares with other preys, is not uniform across the network due to asymmetries in patterns of interaction. We explore the behavior of the system under different interaction strengths and study the dynamics of survival and extinction. In particular, we consider situations in which the four species have initial populations lower than their long-term equilibrium, simulating catastrophic situations in which their abundances are reduced due to human action or environmental change. We show that, under these reduced initial conditions, and depending on the strength of the cross interaction, the populations tend to oscillate before re-equilibrating, disturbing the community equilibrium and sometimes reaching values that are only a small fraction of the equilibrium population, potentially leading to their extinction. We predict that, contrary to one's intuition, the most likely scenario is the extinction of the less predated preys.

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1. Introduction

All living beings interact not only with individuals of its own species, but also with individuals of several other species, forming complex ecological networks [1]. Food webs, in particular, have been recognized as a central representation of ecological communities [2], displaying highly inhomogeneous interactions that are, nevertheless, not random [3]. In fact, several studies have shown that the topology of these networks, e.g., the way links are distributed between species, depends strongly on the predominant type of interspecies interactions [4]. In this sense, asymmetries, in which interacting species differ in their number or intensity of interactions, are particularly common in nature [5]. Different types of mutualism are known to exhibit a nested distribution of links, in which asymmetric interactions among generalists and specialists are pervasive [6–9]. Asymmetries are also widespread in antagonistic interactions, such as herbivory [10], parasitism [11] and predation [12]. Two important issues in ecology regarding network topology are the understanding of how co-evolutionary processes lead to the observed structures and the relation between robustness and stability of networks and its distribution of links [13–16]. These topics are particularly important to conservation biology and also to understand extinction processes that happened in the past [17,18]. In this work we investigate the role of network topology, especially asymmetries, in the
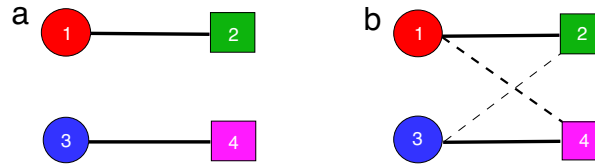

Fig. 1. The four species network: preys are represented by circles, predators by squares and couplings by lines. Each prey, labeled 1 and 3, is coupled primarily to a single predator, labeled 2 and 4. The left panel shows the uncoupled predator–prey pairs, whereas the panel on the right shows the additional asymmetric coupling between predator 4 and prey 1 (thick dashed line). When the coupling between predator 2 and prey 3 (thin dashed line) is also present we term the interaction symmetric.

stability of small predator–prey networks. We simulate the dynamics of a four species network consisting of two predator–prey pairs connected by an asymmetric interaction where the predator of the first pair also feeds from the prey of the second pair (Fig. 1). We show that for a wide range of parameters the system is stable, in the sense that the populations tend to equilibrate at stationary values if slightly displaced from their equilibrium positions. However, if species are displaced from their equilibrium by considerable amounts, like in a catastrophic event caused by human action or environmental change, the populations may oscillate wildly before re-equilibrating, sometimes reaching such low values that Allee effects would drive the population to extinction [19]. In order to take Allee effects into account we introduce an extinction threshold, which is a cutoff value to the dynamics, so that when a population becomes smaller than a certain percentage of its equilibrium value, it automatically goes extinct. We show that such extinction events depend on the strength and topology of connections. This model is minimal, showing several implicit assumptions (e.g., set of interactions and interaction coefficients, parameters of growth and mortality rates of species). Nevertheless, it shows great flexibility making it possible to explore the role of the cross interactions between two primary predator–prey pairs in the stability of the network, representing a first step to understanding the effects of connections between species in the network.

2. A four species model

Our study is based on the classical Lotka–Volterra predator–prey model [20] extended to larger number of species. The equations describing the interactions between preys x_i and predators y_j are

$$\dot{x}_i = \mu x_i(1 - x_i/K) - \sum \mathcal{C}_{ij}x_iy_j,$$
$$\dot{y}_j = -\mu_p y_j + \sum \mathcal{C}_{ji}y_jx_i \tag{1}$$

where μ is the intrinsic growth rate of preys, μ_p is the rate of mortality of predators and K is the local capacity of the preys in isolation. The growth rate of preys is controlled by the logistic term, $(1 - x_i/K)$; and $\mathcal{C}_{ij}$ and the coefficients $\mathcal{C}_{ij}$ and $\mathcal{C}_{ji}$ represent the preys' losses due to predation and the corresponding predators' benefits, respectively. In this model, interspecific competition between different predators arises naturally through the corresponding reduction in the prey population and also through indirect effects, as we will see. In this work we study the simplest case of a four species network, with two identical predator–prey pairs, as illustrated in Fig. 1(a), and coupled as in Fig. 1(b). Although simple, this system can be viewed as a motif [21], a basic unit of species interaction in more complex networks involving larger number of species, allowing the study of predator disturbances in a simplified framework [22]. In the case of four species we can rewrite Eq. (1) using x_1 and x_3 for preys and x_2 and x_4 for predators as

$$\dot{x}_1 = \mu x_1\left(1 - \frac{x_1}{K}\right) - \mathcal{C}_{12}x_1x_2 - \mathcal{C}_{14}x_1x_4$$
$$\dot{x}_2 = -\mu_p x_2 + \mathcal{C}_{21}x_2x_1 + \mathcal{C}_{23}x_2x_3$$
$$\dot{x}_3 = \mu x_3\left(1 - \frac{x_3}{K}\right) - \mathcal{C}_{32}x_3x_2 - \mathcal{C}_{34}x_3x_4 \tag{2}$$
$$\dot{x}_4 = -\mu_p x_4 + \mathcal{C}_{41}x_4x_1 + \mathcal{C}_{43}x_4x_3$$

where $x_1 - x_2$ and $x_3 - x_4$ form the primary prey–predator pairs.

Because of the large number of parameters involved, in our simulations we have fixed $\mathcal{C}_{12} = \mathcal{C}_{34} = 0.05$, $\mathcal{C}_{21} = \mathcal{C}_{42} = 0.02$, $K = 1000$, $\mu = 0.3$, $\mu_p = 0.05$ and studied the system properties as a function of the other four parameters coupling the primary pairs, $\mathcal{C}_{14}$, $\mathcal{C}_{41}$, $\mathcal{C}_{23}$ and $\mathcal{C}_{32}$. The role of the fixed parameters on the dynamics, particularly the role of K, will be discussed later. The fixed parameters $\mathcal{C}_{ij}$ correspond to the interactions within each primary pair and their values have been chosen so as to have stable equilibria. Small variations in these parameters do not cause qualitative change. The role of the carrying capacity, on the other hand, is crucial and is discussed in the next section.

3. Coupling the primary predator–prey pairs

The main point of this article is to understand the effects of cross interaction between otherwise isolated pairs of preys and predators. In the simple case of two pairs considered here, this cross interaction can occur in only two forms, that we
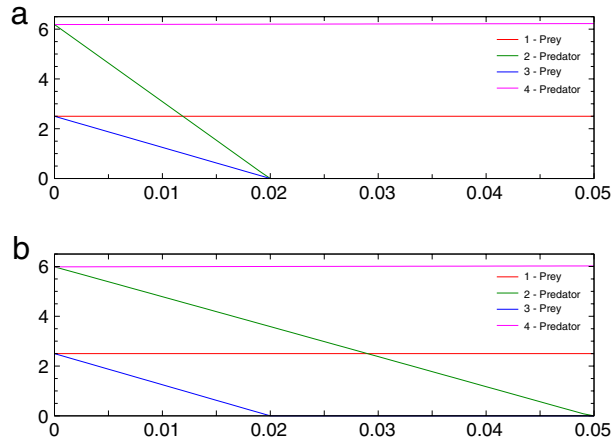
Fig. 2. Equilibrium populations as a function of $\mathcal{C}_{41}$ for (a) unequal asymmetric interaction, $\mathcal{C}_{14} = 2.5\mathcal{C}_{41} =$ and; (b) equal asymmetric interaction, $\mathcal{C}_{14} = \mathcal{C}_{41}$.
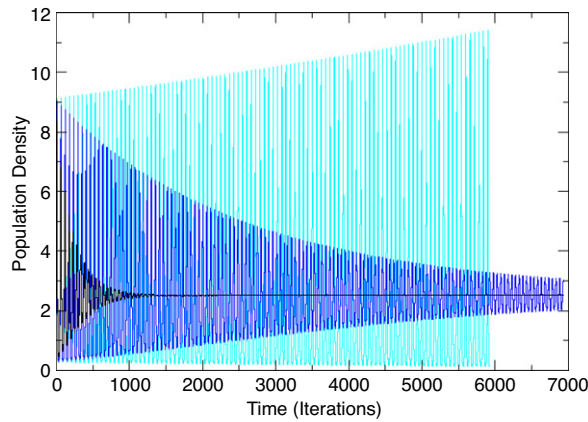

Fig. 3. The role of K in population oscillations. Curves show the population of preys x_1 for the case of non-interacting pairs. For $K = 100$ (black) the oscillations have low amplitude; for $K = 1000$ (blue) the amplitude increases but the population still converges to a stationary equilibrium; for $K = 10{,}000$ (cyan) the amplitude of the oscillations increases considerably and a limit cycle appears. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

term (a) *asymmetric*—one of the predators feeds from both preys whereas the other feeds only from its primary prey or (b) *symmetric*—both predators consume both preys. These situations are illustrated in Fig. 1 where cross interactions are represented by dashed lines. For each of these situations, the effect of cross predation on the corresponding prey and predator may still have different intensities. Here we consider the following four situations:

  (i) non-interacting pairs, as a reference case, where $\mathcal{C}_{14} = \mathcal{C}_{41} = \mathcal{C}_{23} = \mathcal{C}_{32} = 0$.
 (ii) asymmetric, unequal interaction, where $\mathcal{C}_{23} = \mathcal{C}_{32} = 0$ and $\mathcal{C}_{14} > \mathcal{C}_{41}$.
(iii) asymmetric equal coupling, where $\mathcal{C}_{23} = \mathcal{C}_{32} = 0$ and $\mathcal{C}_{14} = \mathcal{C}_{41}$.
(iv) symmetric, equal interaction, where $\mathcal{C}_{14} = \mathcal{C}_{41} = \mathcal{C}_{23} = \mathcal{C}_{32} \neq 0$.

For each of these situations we have calculated the equilibrium populations (Fig. 2) and, more importantly, studied the dynamics under the influence of catastrophic events. In particular, we have calculated the time evolution for the situation in which all four species have initial populations below their equilibrium values, simulating a scenario in which abundances were reduced by human impact or environmental change. Under such conditions, the populations tend to oscillate before eventually re-equilibrating again. This happens because the equilibrium solutions are a *stable focus*, meaning that trajectories starting from nearby initial conditions converge to the equilibrium point but do so oscillating. This is similar to an mechanical oscillator subjected to weak dumping. In this process the number of individuals in the populations might reach such small values that the population, in all practical situations, is unable to recover and die out, even though it may mathematically recover and oscillate back to their equilibrium values. The mathematical recover from too low values (see Fig. 3) is, in many scenarios, unrealistic and we remove it by adding an extinction threshold, or cutoff value, to the dynamics. We refer to the causes of such low populations extinctions generically as Allee effects. Therefore, if the population becomes smaller than a certain percentage of its equilibrium value, it automatically dies out. The value of this extinction cutoff might depend on the
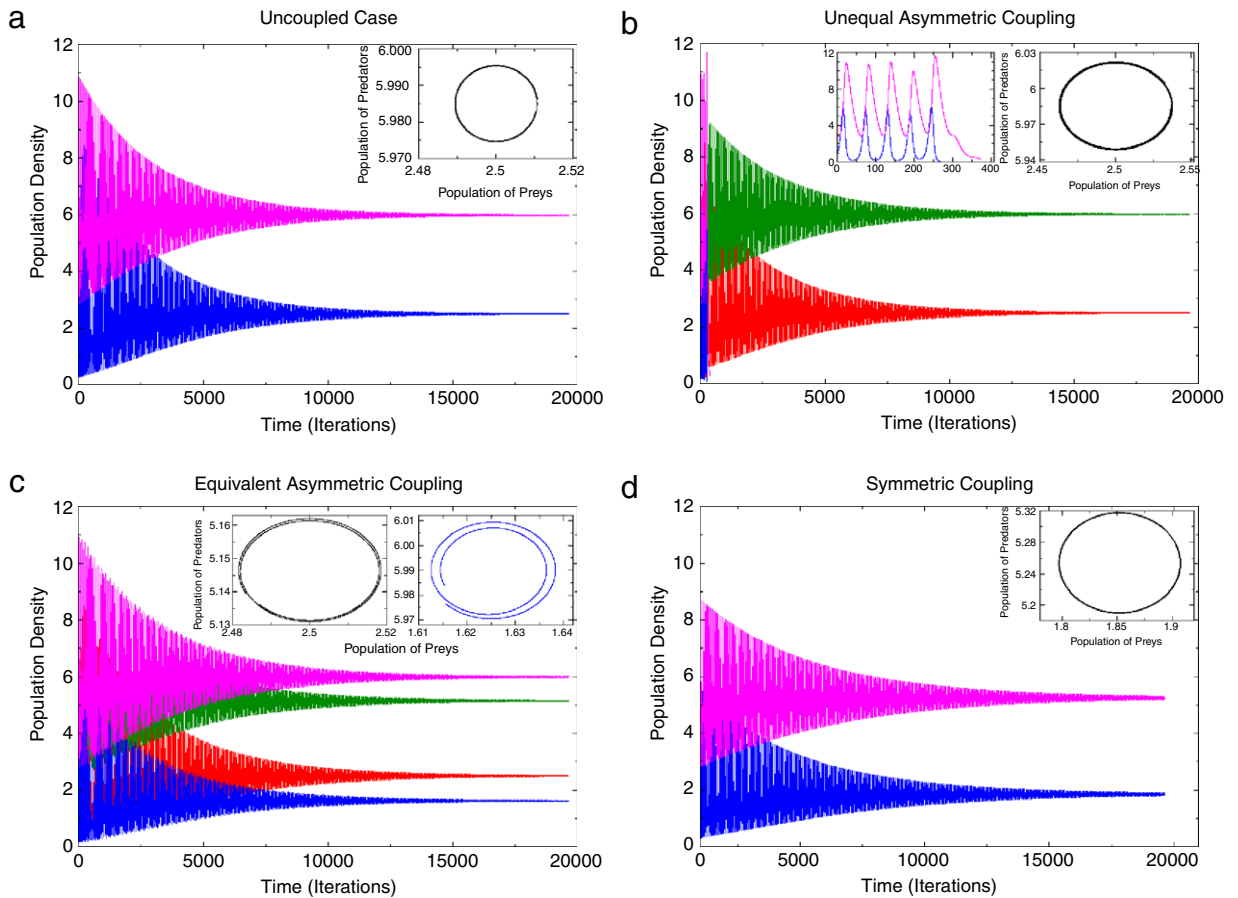
Fig. 4. Time evolution of population densities starting from 50% of equilibrium densities. Colors are as given in Fig. 1. Top left: uncoupled case, inset shows phase space trajectory; top right: unequal asymmetric coupling, insets show short time dynamics and phase space; bottom left: equal asymmetric coupling, insets show phase space for each primary pair; bottom right, symmetric coupling, inset shows phase space.

species and on the environmental conditions. However, in order to simplify the calculations, we used only uniform cutoff values of 5% and 20% of the equilibrium values for all species involved.

Before discussing extinctions caused by oscillations and Allee effects, we turn to the role of the carrying capacity K. The value we use here, $K = 1000$, imply that resources for the preys are abundant by still limited. Fig. 3 shows those larger values of K causes larger amplitudes of oscillations for initial conditions out of equilibrium. For $K = 10,000$ the oscillations not only have very large amplitude but persist as a limit cycle, while for $K = 100$ the oscillations are still present, but have lower amplitude and die out faster. The value $K = 1000$ is intermediate between these two situations.

Within this scenario we have studied the extinction patterns caused by gradual deficits in the initial population densities, varying the initial conditions from 100% to 22%, 5% of their equilibrium values and considering extinction thresholds of 5% and 20%. These scenarios simulate different situations in which the populations decrease due to an external factor, such as human impact (e.g., hunting) or environmental shift leading individuals to die off.

For each of the four types of interactions listed above we show an example of time evolution (Fig. 4) and present the results on extinction in the form of two different diagrams, shown in Figs. 5 and 6. In these diagrams the axes represent the initial population of predators (horizontal) and preys (vertical) in terms of percentage of the corresponding equilibrium values. The outcome of the simulations can be of several types, depending on the type of interaction, on the value of the initial conditions and on the extinction threshold: all species recover their equilibrium values; all species go extinct; only the first predator–prey pair survives; only the second predator–prey pair survives; only the preys survive.

In order to compare the results for the different cutoff values we superimposed the diagrams for 5% and 20% in Fig. 5. The regions of the diagram marked black and blue represent total extinction or survival of the four species, respectively, for both values of the cutoff. The other colors have the following meaning:

Red — survival of all species for 5% cutoff and total extinction for 20% cutoff.
Light gray — survival of only the first pair for 5% cutoff and total extinction for 20%.
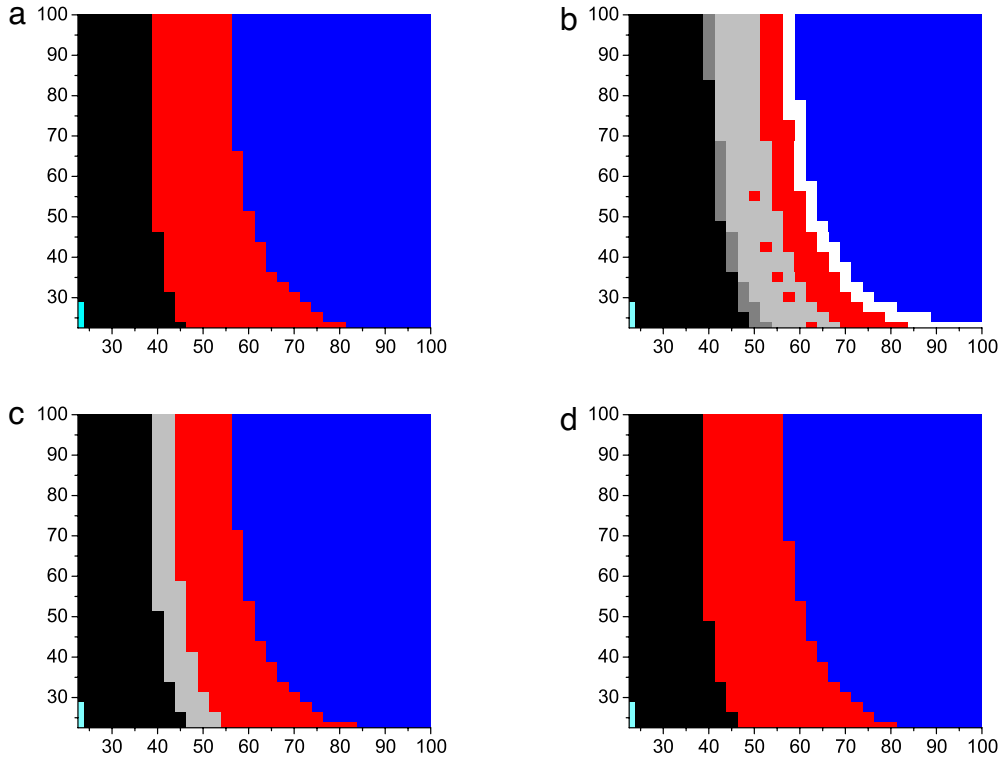White — survival of only the first pair for 20% cutoff and survival of all species for 20%.

Fig. 5. Extinction diagrams for 5% and 20% extinction thresholds. Axis represents initial populations in terms of percentage of the equilibrium values for predators (horizontal) and preys (vertical). (a) *Non-interacting* system; (b) *unequal asymmetric* interaction; (c) *equal asymmetric* interaction and; (d) *equal symmetric* interaction. Blue and black represent regions where all species survive or all die respectively for both cutoff values. The other colors signify: red, survival of all species for 5% cutoff and total extinction for 20% cutoff; light gray, survival of only the first pair for 5% cutoff and total extinction for 20%; white, survival of only the first pair for 20% cutoff and survival of all species for 20%; dark gray, survival of only the second pair for 5% cutoff and total extinction for 20%; cyan, survival of only the populations of preys for 20% cutoff and total extinction for 5%. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Dark gray — survival of only the second pair for 5% cutoff and total extinction for 20%.

Cyan — survival of only the populations of preys for 20% cutoff and total extinction for 5%.

These diagrams allow us to understand the connection between human or environmental impact on survival depending on the ability to recover of the four species involved. We complement these results with Fig. 6, which compares the extinction diagrams for each type of crossed interaction with the reference case for 5% and 20% cutoffs. Like in Fig. 5 the regions marked black and blue represent total extinction or survival of the four species, respectively, for both values of the cutoff. However, the other colors have the following slightly different meaning:

Red — survival of all species for the reference case and total extinction for the corresponding coupled case.

White — survival of only the first pair for the corresponding coupled case and survival of all species for the reference case.

Dark gray — survival of only the second pair for the corresponding coupled case and survival of all species for the reference case.

Cyan — survival of only the populations of preys.

The detailed results for each of the four types of interactions considered are discussed below.

3.1. Non-interacting pairs

Here the predator–prey primary pairs are independent of each other, as in Fig. 1(a), and corresponds to the reference for comparison with the other cases. The dynamic equations for the first pair (the second pair follows identical dynamics) is given by

$$\dot{x}_1 = \mu x_1 \left(1 - \frac{x_1}{K}\right) - \mathcal{C}_{12} x_1 x_2$$
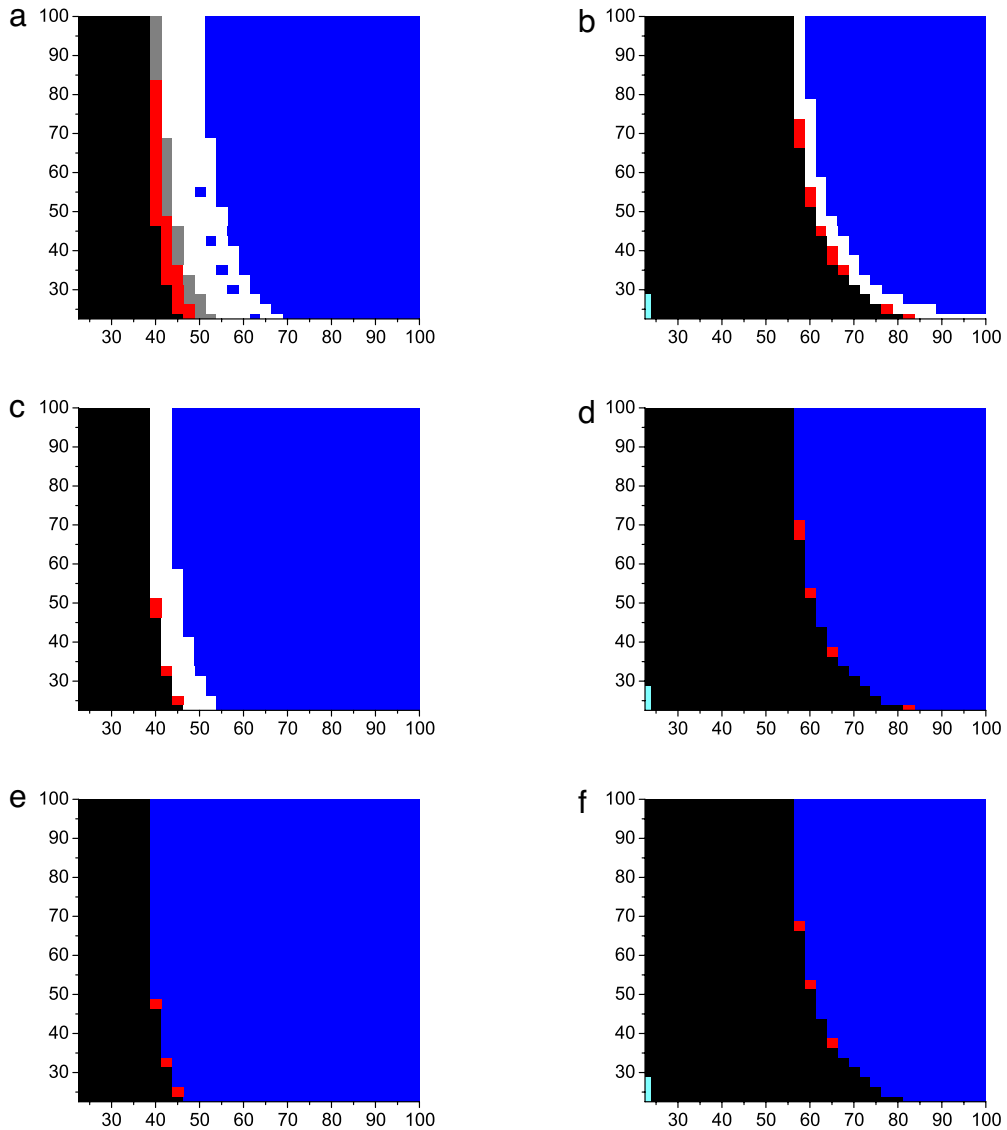$$\dot{x}_2 = -\mu_p x_2 + \mathcal{C}_{21} x_2 x_1$$

(3)

Fig. 6. Extinction diagrams with 5% cutoff (left) and 20% cutoff (right). The results are comparisons between coupled and uncoupled cases: (a) and (b) *unequal asymmetric* coupled case; (c) and (d) *equal asymmetric* coupled case; and (e) and (f) *symmetric* coupled case. Blue and black represent regions where all species survive or all die respectively with and without the coupling. Red indicates survival of all species for the reference case and total extinction for the corresponding coupled case. The other colors represent: white, survival of only the first pair for the interacting case and survival of all species for the reference case; dark gray, survival of only the second pair for the interacting case and survival of all species for the reference case; cyan, survival of only the populations of preys. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with equilibrium populations

$$x_1^{eq} = x_3^{eq} = \frac{\mu_p}{c_{21}}, \qquad x_2^{eq} = x_4^{eq} = \frac{\mu}{c_{12}}\left(1 - \frac{x_1^{eq}}{K}\right). \tag{4}$$

Fig. 4 shows the time evolution of the populations for initial conditions set to 50% of the equilibrium values. As expected, the populations oscillate before re-equilibrating. The population of preys, in particular, reaches very low values. The inset shows the evolution in the phase space of preys (*x*-axis) and predators (*y*-axis).

Fig. 5(a) shows the extinction diagram for 5% and 20% cutoffs superimposed. As expected, species go extinct more easily for 20% extinction threshold, corresponding to a lower ability to recover, than for 5%. The survival of all species for 5% cutoff and total extinction for 20% cutoff (the red area of the figure) represents approximately 26% of the total area.

3.2. Asymmetric interaction

Asymmetric interaction occurs when the predator of the first pair feeds from the prey of the second pair, as illustrated by the thick dashed line in Fig. 1(b). In this case there is a predator with greater benefit and a prey with greater loss. The equations describing this scenario are

$$
\begin{aligned}
\dot{x}_1 &= \mu x_1 \left(1 - \frac{x_1}{K}\right) - \mathcal{C}_{12} x_1 x_2 - \mathcal{C}_{14} x_1 x_4 \\
\dot{x}_2 &= -\mu_p x_2 + \mathcal{C}_{21} x_2 x_1 \\
\dot{x}_1 &= \mu x_3 \left(1 - \frac{x_3}{K}\right) - \mathcal{C}_{34} x_3 x_4 \\
\dot{x}_4 &= -\mu_p x_4 + \mathcal{C}_{41} x_4 x_1 + \mathcal{C}_{43} x_4 x_3
\end{aligned}
\tag{5}
$$

and the equilibrium populations are given by (see Fig. 2)

$$
\begin{aligned}
x_1^{eq} &= \frac{\mu_p}{\mathcal{C}_{21}} \\
x_2^{eq} &= \frac{\mu}{\mathcal{C}_{12}} \left(1 - \frac{x_1^{eq}}{K}\right) - \frac{C_{14}}{C_{12}} x_4^{eq} \\
x_3^{eq} &= \frac{\mu_p}{\mathcal{C}_{43}} \left(1 - \frac{C_{41}}{C_{21}}\right) \\
x_4^{eq} &= \frac{\mu}{\mathcal{C}_{34}} \left(1 - \frac{x_3^{eq}}{K}\right).
\end{aligned}
\tag{6}
$$

3.2.1. Unequal asymmetric interaction

The unequal asymmetric interaction occurs when the ratio between benefit and loss for the predator–prey primary pair is maintained in the interaction of the cross interacting pair. Therefore, the crossed interaction coefficients are unequal and we have set their ratio to $\mathcal{C}_{14} = 2.5\mathcal{C}_{41}$ with $\mathcal{C}_{14} = 0.0175$ and $\mathcal{C}_{41} = 0.007$.

The variation of the equilibrium populations with $\mathcal{C}_{14}$ is shown in Fig. 2(a). The equilibrium population of preys of the first pair remains constant and that of predators of the second pair is also nearly independent of the coupling coefficient, as a large environmental carrying capacity keeps the contribution of other populations insignificant. Furthermore, the two other populations decrease linearly until their extinction, so that for large values of $\mathcal{C}_{41}$ only the preys from the first pair and the predators from the second pair, i.e., the crossed pair, prevail as a new stable predator–prey pair.

The time evolution of the populations for initial conditions equal to 50% of the equilibrium values, Fig. 4(b), shows the second pair going rapidly to extinction, also shown in the phase space plot on the left inset, while the first pair perpetuates. The right inset represents the phase space for the first pair. Therefore, the first pair is more stable than the second, even if its predator feeds only from the prey which is doubly predated. This is a non-intuitive result that can be explained in terms of indirect cross interactions. Indeed, the rapidly increase in the density of the second predator leads its primary prey to extinction, which in turn leads to its own extinction. This is seen more clearly in the left inset, showing the short time evolution of the second pair.

Fig. 5(b) shows the extinction diagram. Here, four new situations arise as compared to the reference case, depending on the value of the cutoff: survival of the first primary pair only, for 5% (light gray), and for 20% (white); survival of the second pair only, for 5% (dark gray); and survival of preys only, for 20% (cyan). The subset of initial conditions leading to the survival of only the second pair is very small: even though this is the most benefited pair, the subset represents only about 2.5% of the area in the plot. For 20% extinction threshold the death rate totally suppresses the survival of only the second pair.

Fig. 6(a) and (b) show the extinction diagrams for 5% and 20% cutoffs, respectively, superimposed with the non-interacting reference case. These figures show the increase in system complexity caused by the crossed interaction. For 5% cutoff the region of total survival (blue area) decreases from 77% to 58% and there appears a considerable region in which a single pair survives, taking 16% of the initial conditions considered. In Fig. 5(b), on the other hand, the cross interaction has a smaller effect: the intermediate region (neither black nor blue) diminishes from 5% to zero.

3.2.2. Equal asymmetric interaction

In the case of equal asymmetric interaction the ratio between benefit and loss for the crossed predator–prey are equal, i.e., $\mathcal{C}_{14} = \mathcal{C}_{41} = 0.007$. Fig. 4(c), shows the time evolution of the population densities for this case for initial conditions equal to 50% of the equilibrium values, shown in Fig. 2(b) as a function of $\mathcal{C}_{41}$. Once again we obtain the non-intuitive result that the most generalist predator thrives but it is the least predated prey that has the smallest densities. Although the relative value of the coefficients in this and the previous case of asymmetric interactions are different, the general behavior of equilibrium populations as a function of $\mathcal{C}_{14}$ is similar. The basic difference between these two situations is that the first predator survives for longer intensities of the cross interaction for the equivalent case. The corresponding extinction diagram, Fig. 5(c), shows the disappearance of the white and dark gray regions, implying that the first pair never survives alone for 20% cutoff. The effect of the cross interaction on the extinction diagram (Fig. 5(c) and (d), for 5% and 20%, respectively) is the death of second primary pair for 5% cutoff which does not happen for the case for 20%.

3.3. Symmetric interaction

Here the interaction between the pairs has the same coefficients, i.e., $c_{14} = c_{41} = c_{23} = c_{32} = 0.007$. Therefore, the pairs have identical dynamics.

The equilibrium populations are given by

$$
\begin{aligned}
x_1^{\text{eq}} &= x_3^{\text{eq}} = \frac{\mu_p}{(c_{43} + c_{41})}, \\
x_2^{\text{eq}} &= x_4^{\text{eq}} = \mu \frac{\left(1 - \frac{x_1^{\text{eq}}}{K}\right)}{(c_{12} + c_{14})}.
\end{aligned}
\tag{7}
$$

Fig. 4(d), shows the time evolution of the population densities for one the pairs for initial conditions equal to 50% of the equilibrium values. Although the populations oscillate and recover their equilibrium values similar to the non-interacting case, the time to equilibration is slightly longer here. The inset represents the phase space trajectory.

The extinction diagram in Fig. 5(d) clearly shows that, for 20% extinction threshold, species go extinct more rapidly. The differences between this and the reference case are minor, as can be seen in Fig. 6(e) and (f), for 5% and 20% cutoffs, respectively. Clearly, the effect of cross interaction is smaller, if not insignificant, when the coupling is symmetric.

4. Discussion

Ecological communities form complex networks of interacting species. The number of species involved is usually large and the types of interactions diverse. Studies have shown that the structure of these networks is intimately connected with ecological and evolutionary processes, and understanding their general properties may tell us something about their origin and stability [9,23–25]. In this work we have considered the relation between network structure and stability of species [26] under catastrophic events for a simple predator–prey network with four species. Our first result concerns the equilibrium populations in the presence of crossed interactions between the two primary predator–prey pairs, as displayed in Fig. 2. For small values of the crossed interaction it is the least hunted prey (prey 3, represented by blue lines in the figures) and the single-prey predator (predator 2, green line) that feel the stronger effects, having their population reduced. While a larger population of predator 4 (pink line) is expected, because more food sources are available to it, it is not evident why the more predated prey 1 (red line) turns out to be more abundant than prey 3. As discussed above, this can be explained in terms of indirect effects, since the rapid increase in the density of predator 4 reduces the population of its primary prey, which in turn reduces its own population. This effect may suggest that apparent competition [27] is strongly affecting the fate of interacting species. This effect can also be understood from the equilibrium equations of the asymmetric case, where the density population of the prey 1 is constant and that of predator 4 is very stable, while the equilibrium densities of populations 2 and 3 decrease with the coupling parameter. The analysis of stability with respect to catastrophic events was surprising in two respects. First, our results indicate that the coupling between the pairs makes the system more vulnerable to extinctions in all cases. Second, the effect of the interactions seems to be important only when Allee effects are not. Both these statements can be inferred directly from Fig. 6. The right column shows that the cross interaction is not relevant for stability when Allee effects are important. In this case, where the populations go extinct when reaching 20% of their equilibrium values, the black and blue areas (representing total extinction or total survival with or without the cross interaction) dominate the diagram. For 5% cutoff, however, which models situations where Allee effects are weak and the populations are very resilient, a large part of the diagram corresponds to new outcomes, particularly for asymmetric and unequal interactions, Fig. 6(a). White and gray areas correspond to survival of all species for the uncoupled case but survival of only the first or second pairs respectively for the coupled case. The red correspond to survival of all species for the uncoupled and total extinction for the coupled case. Thus, our results provide an insight on how Allee effects and network topology interacts, leading to distinct dynamics in predator–prey interactions. If these conclusions hold also for more complex networks, the stability of communities may be largely overestimated if interactions between species are neglected.

Our analysis also point to the importance of species-specific characteristics on the patterns of extinctions, as modeled here by the extinction threshold, which quantifies the capacity of a species to recover its equilibrium population from low values. This is evident from Fig. 4, which superimpose the extinction patterns for 5% and 20% cutoffs. The dynamical mechanism that causes extinctions in our model is the oscillations displayed by the populations before equilibrium is achieved, as illustrated in Fig. 2. The larger the amplitude of these oscillations the smaller the populations get and the more susceptible to extinction it becomes. The parameter that control the amplitude the oscillations is the carrying capacity K. In the limit of very large K the populations become unstable and any perturbation can disrupt the system. This is also a non-intuitive result that can be understood as follows: if resources are abundant, the population of preys may increase to large values, leading to an equivalent increase in the population of predators. This, on the other hand, leads to the extinction of the less predated prey, as discussed above, and might also eliminate one of the predators.

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