Population structure plays a key role in community stability

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Abstract

The relationship between ecosystem complexity and stability remains unresolved and a mechanistic explanation for the stunning levels of biodiversity observed in communities and ecosystems is still lacking. Recent work has shown that differences in the foraging capacity and predation risk of juveniles versus adults within populations result in larger, more complex communities than predicted by unstructured models. Here, we develop a general framework to integrate population structure into community stability analyses and show that stage-asymmetric interactions are key to stability. Specifically, while cross-stage predator-prey interactions enhance stability, competition across different stages destabilises the community. Our results offer new insights into the stability-diversity paradox, emphasising the critical role of population structure in ecological resilience, an often neglected feature of natural systems.

Keywords: Community stability, Population structure, Community matrix, Stage-specific interactions, Resilience.

The stability of large ecosystems

The **stability** and **diversity** of ecological communities has been a central question in ecology for decades [1–4]. Although most natural ecosystems are able to maintain their structure and function over time [5, 6], even in the presence of disturbances [7, 8], the mechanisms that promote this stability are not yet fully understood [9]. Ecologists have long argued that **complexity** promotes stability, allowing for a greater number of interactions between species that can buffer the system against disturbances [10]. However, the idea of "higher diversity = higher stability" was challenged over 50 years ago by the theoretical work of Robert May, who showed that large and diverse ecosystems are inherently unstable [11]. This apparent paradox sparked the so-called stability-diversity debate [10], prompting extensive research to uncover the mechanisms that promote stability in ecosystems [6, 12, 13]. However, the contradiction between theory and observation remains unresolved [14–16]. Despite this oversimplified crash history on the complexity-stability debate, the point is clear: a mechanistic explanation for the stunning levels of biodiversity observed in communities and ecosystems is still lacking.

The study of ecological communities has long been dominated by the assumption that populations are homogeneous entities. However, they consist of individuals that differ in multiple traits, such as age, size, and developmental stage, which in turn live in diverse and heterogeneous environments. Recent research has highlighted that this **population structure** can significantly influence ecological dynamics and stability [17–19]. Structured populations can exhibit different interaction strengths, dispersal rates, or mortality risks based on individual characteristics, which ultimately affect species persistence and community-level responses to perturbations [20–22]. For example, asymmetries in the extent of food limitation between individuals in different **life cycle** stages can lead to an

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increase in the efficiency with which resources are used for population growth when conditions change [23]. In fact, recent theoretical work has shown that differences in juvenile foraging capacity and predation risk vs. adults within populations result in larger and more complex communities than predicted by unstructured models [19]. However, these results are limited to a specific model of predator-prey interactions. The generality of such findings for more complex communities that incorporate diversity in species life cycles is currently lacking, despite its suggested potential to bring clarity to the stability-diversity debate [10].

Here, we introduce a general framework to study the role of population structure in the stability of ecological communities. Unlike standard models, which assess interactions at the species level in an unstructured manner, we consider within-population variation due to individual development during the life cycle. Our framework explicitly accounts for inter-stage (e.g., adult-juvenile) and intra-stage (e.g., adult-adult) interactions by taking into account the structures of the populations involved in the community interaction. This layered structure can accommodate any number of life stages for any number of species, and can then be used to systematically integrate this rich information into standard stability analyses. We examine the stability of the community under different types of stage-symmetric and asymmetric interactions. We offer new insights into the stability-diversity paradox, emphasising the potential contribution of population structure in ecological resilience, an often-times neglected feature of natural systems [14, 24, 25]. We finally propose a road map for future research, including extensions to further develop our framework.

Modelling communities with unstructured populations

The stability of ecological communities is often tackled from a **dynamical systems** perspective [26]. Typically, in community ecology, a community is a set of interacting species in which the dynamics of their densities is described by a system of **Ordinary Differential Equations** (ODE). Under this formalism, the **local asymptotic stability** of the system with regards to a given **feasible equilibrium point** is completely determined by the **eigenvalues** of the **Jacobian matrix** of the system evaluated at the equilibrium, also known as the **community matrix** (Box 1). This approach enables the study of the stability of communities in a general and systematic way, and has been instrumental in the development of the field of theoretical ecology [27–31]. While the study of feasibility in ecological communities—examining whether all species maintain positive abundances at equilibrium—is an important and related problem [32, 33], our focus here is solely on stability.

Determining the exact form of the system of ODEs that describe the dynamics of a given species in a community can be challenging. The difficulty in doing so stems from the requirement for detailed knowledge of the interactions between species [34]. Indeed, field data on community interactions are limited by the vast number of potential interactions in diverse communities and the significant effort required to document these interactions [35]. Moreover, the variation in species interactions across space and time adds further complexity [36], making it difficult to distinguish between true negatives (i.e., where species do not interact) and false negatives (where interactions are present but undetected). Furthermore, empirical estimates of interaction strength are often biased, as they typically rely on species-level summaries, losing critical detail about individual or contextual variations [37]. Consequently, studying the stability of communities with a large number of species has remained a gargantuan task in Ecology.

Over half a century ago, Robert May combined dynamical systems theory with the emergent theory of random matrices to develop a ground-breaking framework to study the stability of ecosystems. This approach is based on the insight of modelling the community matrix as a large **random matrix**, thus overcoming the need to specify the details of the interactions between species by defining a specific system of ODEs from which to obtain the Jacobian [11, 38]. In other words, this model considers that species interact with some probability and then the sign (e.g., negative for competitive or positive for mutualistic) and strength of the interaction are randomly assigned. May's main result showed that a large ecosystem with random interactions is stable with full certainty (probability of stability = 1) whenever the inequality shown below holds.

$$\sigma\sqrt{SC} < 1 \, , \tag{1}$$

where σ is the standard deviation of the interaction strength between species in the community of interest, S is the number of species in the community, and C is the probability of interaction between species (Box 2). Thus large (i.e. $S \to \infty$) and/or complex (very interconnected $C \to 1$ or strongly interacting $\sigma \to \infty$) communities are rather likely to be unstable.

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Box 1: Dynamical systems perspective on assessing ecosystem stability

Consider a community composed by S species in which the dynamics of the species densities, N_i, are described by a general system of ODEs which might depend on the population densities of all species in the community

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = f_i(N_1, \ldots, N_S) . \tag{2}$$

Any equilibrium point of the system is given by the solution of

$$f_i(N_1, \ldots, N_S) = 0 , \tag{3}$$

and is said to be feasible if all species have positive population densities.

To study the stability of the system one can consider the dynamics of small perturbations around a given feasible equilibrium, $\boldsymbol{N}^*$, which are given by

$$\boldsymbol{N}(t) = \boldsymbol{N}^* + \boldsymbol{\xi}(t) . \tag{4}$$

We obtain a linearised approximation of the system by taking a Taylor expansion of the system of ODEs around the equilibrium and discarding higher order terms:

$$\frac{\mathrm{d}\boldsymbol{\xi}(t)}{\mathrm{d}t} = \boldsymbol{M}\boldsymbol{\xi} , \tag{5}$$

where $\boldsymbol{M}$ is the jacobian matrix of the system evaluated at the equilibrium, also known as the community matrix, given by

$$m_{ij} = \left.\frac{\partial f_i}{\partial N_j}\right|_{\boldsymbol{N}^*} . \tag{6}$$

Thus, the elements of the community matrix measure the effect of a small change in the abundance of species j on the growth rate of species i at a given feasible equilibrium.

The solution of the linearised system (5) is given by

$$\xi_i(t) = \sum_{j=1}^{S} C_{ij} e^{\lambda_j t} , \tag{7}$$

where C_{ij} are constants that depend on the initial conditions and λ_j are the eigenvalues of the community matrix M.

Thus, the stability of the system is determined by the sign of the real parts of the eigenvalues of the community matrix. If all eigenvalues have negative real parts, all terms in Eq. (7) decay to zero and the system is locally asymptotically stable. However, if there exists even one eigenvalue with a positive real part, the corresponding term in Eq. (7) grows exponentially, driving the population away from the equilibrium and rendering the system locally unstable.

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May's seminal work has greatly influenced the field of theoretical and applied ecology [39, 40], having inspired a large body of work on the stability of ecosystems [38, 41, 42]. The body of work that has followed has demonstrated how the specific type of inter-specific interaction (e.g., predation, competition, mutualism) is key in determining the stability of the community. For instance, we now know that in communities in which all individuals display the same type of interactions, predator-prey dynamics promote stability, while mutualism and competition destabilise it [43]. At the same time, a proportion of mutualistic interactions in predation networks can be stabilising [44, 45]. Weak species interactions can either stabilise or destabilise a community depending on the

dominant type of interaction [43, 46], while May's stability criteria Eq. (1) are unaffected by the inclusion of explicit density-dependent interactions [47].

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Box 2: The stability of ecosystems from a random matrix approach

Consider a community composed by S species whose densities obey a given system of ODEs, so that its stability is determined by the eigenvalues of the community matrix $\boldsymbol{M}$. The community matrix can be modelled as a random matrix. Within this classical framework of community ecology [11], it is often assumed that the species are self-regulating (e.g. negatively density-dependent), so that the diagonal elements of the community matrix are negative, usually set to a constant value $\boldsymbol{M}_{ii} = -d$. Species interact with probability C and different types of interactions can be modelled by specifying the sign relation between the off-diagonal elements of the matrix [43]

- **Competition:** $\text{sign}(m_{ij}) = \text{sign}(m_{ji}) = -$
- **Mutualism:** $\text{sign}(m_{ij}) = \text{sign}(m_{ji}) = +$
- **Predation:** $\text{sign}(m_{ij}) = -\text{sign}(m_{ji})$

where the coefficients m_{ij} can be thought of as the effect of the abundance of species j on the growth rate of species i.

Using tools from random matrix theory, one can study the statistical properties of the eigenvalues of the community matrix and determine the conditions under which the system is stable. For example, the eigenvalue distribution of a $S \times S$ random matrix $\boldsymbol{M}$ with independent and identically distributed entries of zero mean, and variance σ and with trace $\text{Tr}(\boldsymbol{M}) = \sum_i m_{ii} = d$ converges to a uniform distribution in a circle in the complex plane with centre $(d, 0)$ and radius $\sigma\sqrt{SC}$ as $S \to \infty$ [38, 48]. Here σ can be understood as the interaction strength between species, and we note that the outcome is independent from the probability distribution from which the matrix elements are obtained.

This result is key to examine the stability of communities with random species interactions (i.e. a combination of mutualism, competition, and predation), in which the elements of the community matrix are given by [11, 38]

$$\boldsymbol{M}_{ij} \sim \mathcal{D}(0, \sigma^2) \quad \text{with probability } C \text{ or } 0 \text{ otherwise} \quad \forall i \neq j$$
$$\boldsymbol{M}_{ii} = -d \tag{8}$$

where $\mathcal{D}$ is any probability distribution with finite first and second moments (e.g. a Gaussian).

In this case, the eigenvalues of the community matrix will be uniformly distributed in a circle of radius $\sigma\sqrt{SC}$ centered at $(-d, 0)$ as $S \to \infty$, which implies that the system will be stable with probability one whenever

$$\gamma = \sigma\sqrt{SC} < d . \tag{9}$$

This inequality is a slight generalisation of May's original stability criterion, γ, which can be recovered by setting $d = 1$. Similar stability criteria can be obtained for specific types of interacting communities [43, 49]:

$$
\begin{aligned}
\textbf{Mutualistic:} \quad & \gamma_m = \sigma C(S-1)\sqrt{\tfrac{2}{\pi}} < d \\
\textbf{Competitive:} \quad & \gamma_c = \sigma\left\{\sqrt{SC}\left(1 + \tfrac{2-2C}{\pi-2C}\right)\sqrt{\tfrac{\pi-2C}{\pi}} + C\sqrt{\tfrac{2}{\pi}}\right\} < d \\
\textbf{Predator-prey:} \quad & \gamma_p = \frac{\pi - 2}{\pi}\sigma\sqrt{SC} < d
\end{aligned}
\tag{10}
$$

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Several mechanisms affecting community stability have been hitherto identified, such as omnivory [50], the compartmentalization or patterning of species interaction [46, 51–53], adaptive foraging [54], allometric scaling of predator-prey interaction strength [55] or the structure of the interaction network [56]. In addition, the fact that interactions among species are not always pair-wise, but rather higher-order [57], and that the effect of the interactions is not instantaneous but can occur with a delay [42], has also been shown to build more robust and stable communities. Even recent considerations on the role of **transient dynamics** [30, 58] have been incorporated into the framework by means of **pseudospectral analysis** [59, 60], showing that **reactivity** is an intermediate state between non-reactivity and instability that could be used as an early-warning signal for ecosystem collapse. However, despite all these advances, May's main result, that

complexity begets instability, still holds. Thus, the stability-diversity paradox remains.

Towards the inclusion of structured populations

Individual heterogeneity within natural populations is ubiquitous in nature [22]. A key expression of such heterogeneity arises from life cycles, which encapsulate the series of developmental stages and life history strategies that individuals progress through during their lifetime. These life cycles dictate how key **vital rates** like survival, growth, and reproduction vary across different stages, shaping the ecological roles individuals play throughout their ontogeny [21, 61, 62]. For example, reproductive output peaks shortly after the age of first reproduction and then slowly decreases in asexually reproducing monogonont rotifers [63, 64]. In many plants, survival is strongly size-dependent [65], while insects have different developmental stages that may differ significantly in their size, diet, and, as a result, their survival probabilities [66]. Indeed, asymmetric intra-specific competition for resources between different life history stage has been thoroughly documented [67–71], highlighting how life cycle stages contribute to population structure and ecological dynamics.

To accommodate such heterogeneity, population ecologists developed and fully embraced structured population models decades ago [21, 61, 62]. These models explicitly link the value of vital rates (and thus the components of fitness; [72]) to key attributes of the anatomy/physiology of the individual [21, 73]. Indeed, in structured population models, individuals are typically classified by their age, size, or developmental stage, though other traits can be used too [74, 75]. These models are arranged, among others, into matrix population models (MPMs; [21]) if the population classes are discrete, or integral projection models (IPMs; [73]) if the population is classified according to a continuous variable, with transition probabilities also modeled as continuous functions. Surprisingly, after more than 50 years of research on the stability of ecosystems, this key aspect of natural populations, that is their structure, remains largely overlooked. Some specific attempts have been made to understand the effect of population structure on community dynamics [23, 76–78]. However, a comprehensive understanding of how population structure influences the stability of ecological communities, integrating diverse life cycle stages and species interactions, remains an unresolved challenge.

Here, we introduce a generalised framework to examine the stability of communities with structured populations. We consider a community composed by S species and K life cycle stages for each species. These K stages could represent discrete developmental groups–such as juveniles and adults–or age-, sex- and size-based groupings. What matters in this regard is that the groups represent biologically-meaningful differences in the probability, direction, or strength of interactions among the species-stage combinations.

A general framework to address the role of population structure in the stability of communities

Consider a dynamical system representing a community of age/stage-structured populations. Generally, we may consider S species and K stages for each species. The dynamics of the system can be described by a general system of ODEs that describes the growth rate of each population stage as a function of the abundances of all stages of all species (including the focal species) in the community,

$$\frac{\mathrm{d}N_i^{(k)}}{\mathrm{d}t} = g_i^{(k)} \left(N_1^{(1)}, \ldots, N_1^{(K)}, \ldots, N_S^{(1)}, \ldots, N_S^{(K)} \right) \ , \tag{11}$$

where $N_i^{(k)}$ denotes the density of the stage k of species i, with $i = 1, ..., S$ and $k = 1, ..., K$. This set of ODEs can incorporate any desired ecological mechanisms (e.g., transfers between stages due to reproduction or ageing, any explicit functional form of species interaction, etc).

We can rearrange this system of ODEs by defining

$$N_i = \sum_{k=1}^{K} N_i^{(k)} \tag{12}$$

$$Z_i^{(k)} = \frac{N_i^{(k)}}{N_i} \quad \forall k = 1, ..., K-1 , \tag{13}$$

where N_i represents the total density of species i, $Z_i^{(k)}$ is the fraction of population density at stage k of species i. The fraction of population density at stage K is automatically defined by

$$N_i^{(K)} = N_i \left(1 - \sum_{k=1}^{K-1} Z_i^{(k)} \right) \tag{14}$$

We can then express our system of ODEs Eq. (11) as a function of total abundances Eq. (12) and fraction of stages Eq. (13),

$$\begin{aligned} \frac{\mathrm{d}N_i}{\mathrm{d}t} &= f_i \left(N_j, Z_j^{(1)}, \ldots, Z_j^{(K-1)} \right) \\ \frac{\mathrm{d}Z_i^{(k)}}{\mathrm{d}t} &= f_i^{(1)} \left(N_j, Z_j^{(1)}, \ldots, Z_j^{(K-1)} \right) \end{aligned}, \tag{15}$$

where $k \in 1, ..., K-1$ and $j \in 1, ..., S$.

This change of variables is trivial, but crucially important to allowing us to express the upper left sub-matrix of the Jacobian as the traditional community matrix. In this way, we can directly compare the eigenvalues of the traditional community matrix, that does not take into account stage structure, to that of our full stage-structured matrix. In turn, this allows us to understand the effect of population structure on the stability of the community.

We define the structured community matrix, $\boldsymbol{M}_S$ as the Jacobian of the age/stage structured population model evaluated at a feasible equilibrium point (denoted by $*$), which is a $SK \times SK$ matrix given by

$$\boldsymbol{M}_S = \begin{pmatrix} \frac{\partial f_i}{\partial N_j} & \frac{\partial f_i}{\partial Z_j^{(1)}} & \cdots & \frac{\partial f_i}{\partial Z_j^{(K-1)}} \\ \frac{\partial f_i^{(1)}}{\partial N_j} & \frac{\partial f_i^{(1)}}{\partial Z_j^{(1)}} & \cdots & \frac{\partial f_i^{(1)}}{\partial Z_j^{(K-1)}} \\ \vdots & & & \vdots \\ \frac{\partial f_j^{(K-1)}}{\partial N_j} & \frac{\partial f_j^{(K-1)}}{\partial Z_j^{(1)}} & \cdots & \frac{\partial f_j^{(K-1)}}{\partial Z_j^{(K-1)}} \end{pmatrix}^* = \begin{pmatrix} \boldsymbol{M} & \boldsymbol{M}_S^{12} & \cdots & \boldsymbol{M}_S^{1K} \\ \boldsymbol{M}_S^{21} & \boldsymbol{M}_S^{22} & \cdots & \boldsymbol{M}_S^{2K} \\ \vdots & & & \vdots \\ \boldsymbol{M}_S^{K1} & \boldsymbol{M}_S^{K2} & \cdots & \boldsymbol{M}_S^{KK} \end{pmatrix} \tag{16}$$

in which each element of the depicted matrix is, in turn, a $S \times S$ matrix. Note that the sub-matrix $\boldsymbol{M}_S^{11}$ of the structured community matrix, $\left(\frac{\partial f_i}{\partial N_j} \right)^*$, is the usual community matrix, $\boldsymbol{M}$, representing the interactions between total species abundances. The remaining sub-matrices represent the interactions between stages of the species.

The stability of the system is determined by the eigenvalues of the structured community matrix, $\boldsymbol{M}_S$, which generalises the community matrix to structured populations. Our framework can also accommodate species with differing number of life cycle stages. To do so, one only needs to develop the model for K_{max} stages (where K_{max} denotes the maximum number of life cycle stages of any species' population in the community) and set to 0 the interaction coefficient of the non-existing stages of populations with a number of stages smaller than K_{max}.

The approach of random matrices can be applied to the structured community matrix, allowing the study of the stability of ecological systems with structured populations in a general and systematic way. However, obtaining a general analytical solution for the stability criterion of communities with structured populations is arduous. In the following, we present some examples of how population structure can influence the stability of communities, showing that one can obtain opposite results when considering unstructured models.

Asymmetry between intra- and inter-stage interaction types is key to community stability

Our framework is general and flexible, capable of modelling any type of interaction among population stages within or across species in a community. To illustrate its utility, we analyse the simplest scenario: communities comprising populations structured into two stages. Here these stages represent age (e.g., adults and juveniles), sex (e.g., males and females), or other traits; for clarity, we refer to juvenile and adult stages throughout. This setup allows us to systematically explore the effects of stage-specific interactions, such as mutualistic (+/+), competitive (-/-), or trophic (e.g., predator-prey) relationships, on overall community stability. For instance, we investigate cases where adult-adult interactions are competitive while adult-juvenile interactions are predatory, cases where adult-adult interactions are mutualistic while adults compete with juveniles... demonstrating the versatility of the framework in analysing diverse interaction configurations. Detailed information on the parametrization of the structured community matrix for each case is provided in Supplementary Sections 1 and 2.

In Fig. 2, we show the comparison of the stability outcomes of structured and unstructured communities, highlighting how distinguishing life stages can reshape stability predictions. One key finding is that when inter- and intra-stage interactions are of the same type (e.g., all competitive), introducing population structure has little to no effect on community stability (Fig. 2 and Supplementary Fig. 1). However, when inter- and intra-stage interaction types differ, novel stabilising or destabilising mechanisms emerge. For example, we recover the results of de Roos [19] by incorporating predator-prey interactions between adults and juveniles of different species (Box 3). These inter-stage predator-prey interactions stabilise the community, regardless of the nature of intra-stage interactions (Fig. 2 and Supplementary Fig. 2). Conversely, we show that competition across life stages consistently promotes instability (Fig. 2 and Supplementary Fig. 3).

Box 3: Cross-stage predator-prey interactions stabilise communities

To demonstrate the applicability of our approach, we extend the insights of de Roos [19] to a broader context. Using a specific system of differential equations, de Roos highlighted that the differential foraging abilities and predation risks between juvenile and adult individuals within populations can enhance community stability. In this example, we parametrise our general model to represent a community featuring adult-juvenile predator-prey interactions, while adult-adult and juvenile-juvenile interactions are treated as random, allowing for any sign in their interaction strengths. In this particular case the structured community matrix is a simpler $2S \times 2S$ matrix, which can be expressed as the following 2×2 block matrix (of $S \times S$ sub-matrices),

$$M_S = \begin{pmatrix} M_1 & M_2 \\ M_3 & M_4 \end{pmatrix} = \begin{pmatrix} M & M_2 \\ M_3 & M_4 \end{pmatrix} \tag{17}$$

$M_1 = M$ is the traditional community matrix, and it represents the pair-wise interactions between the populations of two different species within the community, where the interaction does not take into consideration the structure of either species' population. M_2 represents the interactions between the total population of one species and the fraction of juveniles of another. M_3 represents the interactions between the fraction of juveniles of one species and the total population of another. Finally, M_4 represents the interactions between the fractions of juveniles in pair-wise combinations of species in the community.

To demonstrate the impact of population structure on community stability, we explored how interactions between different life cycle stages influence the overall dynamics. We first considered random species interactions in M_1 and M_4, and predator-prey interactions in M_2 and M_3. As such, the diagonal elements of M_1 and M_4 were set to $-d$, corresponding to density-dependent regulation in each stage, while their off-diagonal elements were drawn from normal distributions with mean zero and variance σ_1 and σ_4, respectively. In contrast, the elements of M_2 and M_3 were obtained by considering that whenever species i is a predator of species j, $m_2^{ij} \sim |\mathcal{N}(0,\sigma_2)|$, $m_2^{ji} \sim -|\mathcal{N}(0,\sigma_2)|$, $m_3^{ij} \sim -\mathcal{N}(0,\sigma_3)$ and $m_3^{ji} \sim |\mathcal{N}(0,\sigma_3)|$. Thus, each of the sub-matrices is parametrised by σ_i, but because S and C are fixed parameters, they can also be parametrised in terms of γ_i Eq. (10): $\gamma_1 = \sigma_1\sqrt{SC}$, $\gamma_2 = \frac{\pi-2}{\pi}\sigma_2\sqrt{SC}$, $\gamma_3 = \frac{\pi-2}{\pi}\sigma_3\sqrt{SC}$ and $\gamma_4 = \sigma_4\sqrt{SC}$. Thus,

γ_1 and γ_4 represent the interaction strength between individuals sharing the same stage while γ_2 and γ_3 represent the cross-stage interaction strength. Detailed information on the parametrization of the structured community matrix is provided in Supplementary Section 2.
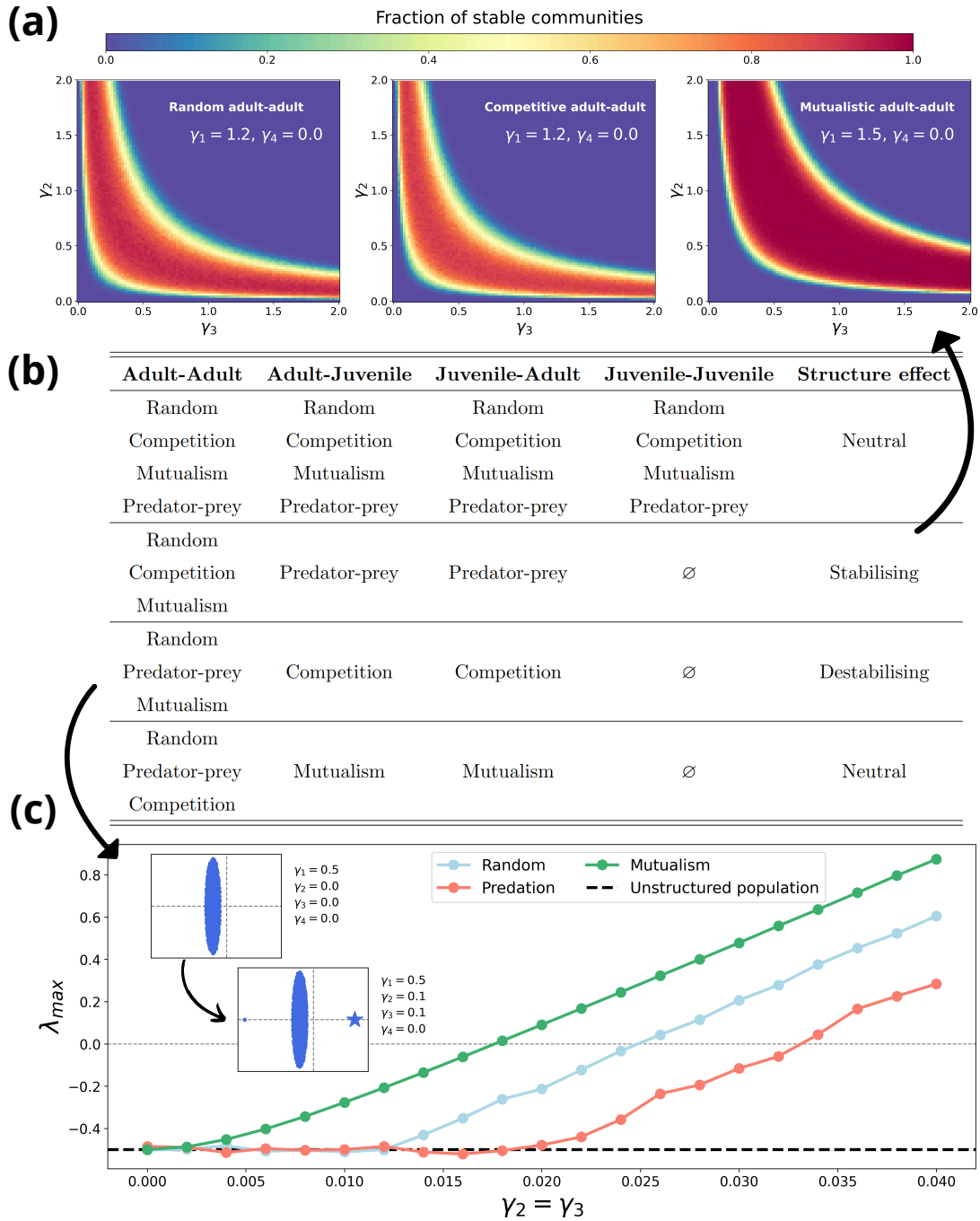
The key consideration is that we set $\gamma_1 > d$ (i.e., the interaction strength among the total population abundances exceeds the self-regulation capacity of each population), and as such $M_1 = M$ has at least one positive eigenvalue. If we only consider the interactions among the total population abundances in the community (the sub-matrix $\boldsymbol{M_1}$ in Eq. (17)), we would conclude that the community is unstable. However, when explicitly considering population structure, the stability of the community depends on the cross-stage interaction strength, γ_2 and γ_3 (Fig. 1). We reach the same conclusion when the adult-adult interactions are set to be competitive or mutualistic (Supplementary Fig. 2).
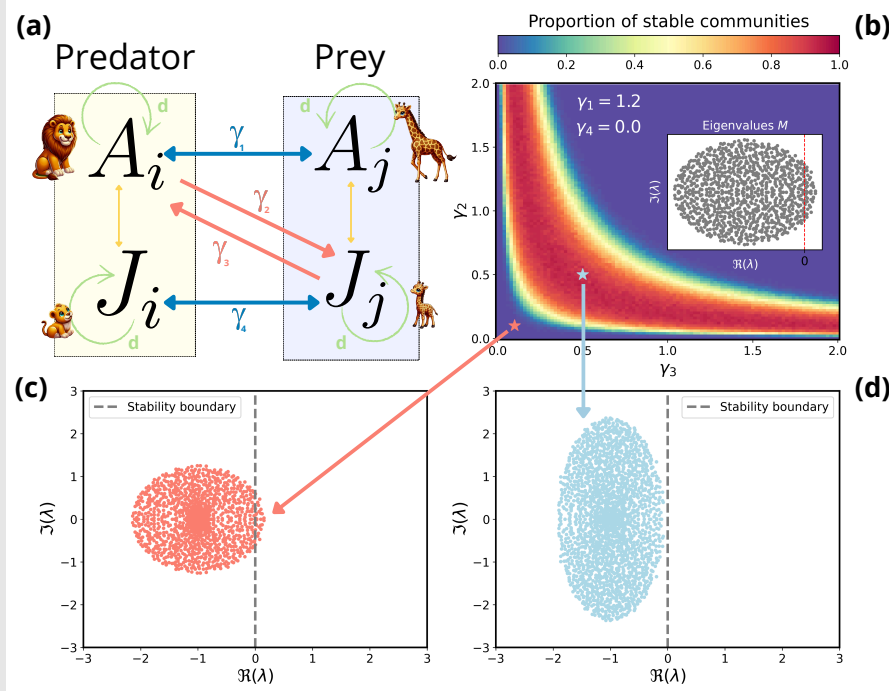
Figure 1: Stability analysis of a community composed by structured populations (adults and juveniles) with cross-stage predator-prey interactions. (a) Adult-adult and juvenile-juvenile interactions between species are set randomly, so any interaction type can occur, while adult-juvenile interactions between species are predator-prey. (b) Proportion of stable communities as a function of the adult-juvenile predatory-prey interaction strengths, γ_2 and γ_3. The total population to total population interaction strength is set to $\gamma_1 = 1.2$, which is higher than the self-regulation term, $d = 1$. The juvenile-juvenile interaction strength is set to $\gamma_4 = 0$, so juveniles do not interact with other juveniles. The traditional community matrix that considers unstructured populations ($\gamma_1 = 1.2$) has positive eigenvalues (inset) so that the community would be labeled as unstable. However, there is a region of stability. (c) Eigenvalues of the structured community matrix for $\gamma_2 = \gamma_3 = 0.1$. The cross-stage interaction strength is not enough to provide stability to the community. (d) Eigenvalues of the structured community matrix for $\gamma_2 = \gamma_3 = 0.5$. The cross-stage predator-prey interactions provide stability to the community.

Interestingly, our results show that mutualistic cross-stage interactions have minimal influence on community stability compared to unstructured models (Fig. 2 and Supplementary Fig. 4). This result suggests that the stabilising effects of population structure depend critically on the asymmetry and regulatory dynamics introduced by specific interaction types. These findings underscore the importance of explicitly considering life cycle stage heterogeneity in ecological models, paving the way for more accurate predictions of community stability across diverse ecological contexts.

(a)

Fraction of stable communities

Adult-Adult	Adult-Juvenile	Juvenile-Adult	Juvenile-Juvenile	Structure effect
Random	Random	Random	Random	
Competition	Competition	Competition	Competition	Neutral
Mutualism	Mutualism	Mutualism	Mutualism	
Predator-prey	Predator-prey	Predator-prey	Predator-prey	
Random				
Competition	Predator-prey	Predator-prey	$\varnothing$	Stabilising
Mutualism				
Random				
Predator-prey	Competition	Competition	$\varnothing$	Destabilising
Mutualism				
Random				
Predator-prey	Mutualism	Mutualism	$\varnothing$	Neutral
Competition				

(b)

(c)

Figure 2: Effect of adding population structure on the stability of communities. We compared the stability of communities with no population structure (each species is represented only once) to the stability of communities with a juvenile and adult class for each species. We refer to the effect as stabilising when the region of the parameter space where the community is stable is larger for the structured than the unstructured model. We refer to the effect as destabilising when the community with structured populations is unstable in regions of the parameter space where would be stable in the unstructured case. The effect is neutral when the region of stable communities is the same for the structured and unstructured models. The top panels show the stabilising effect of structured predator-prey interactions regardless of the total-population to total-population interaction type. The bottom panel shows the destabilising effect of structured competitive interactions.

Concluding remarks

Our framework provides a general approach to studying the stability of ecological communities with structured populations, extending current approaches from dynamical systems and random matrix theory [11, 19, 38, 43]. Unlike frequently used approaches that treat populations as homogeneous entities [79, 80], our framework integrates heterogeneity to study how age, size, behavioural or other individual traits may modulate community responses to environmental fluctuations. By explicitly integrating biologically meaningful differences across life cycle stages into stability analyses, our framework extends traditional community matrix models to address the complexities inherent in natural ecosystems [18, 23]. The framework allows for the systematic examination of different types of cross-stage interactions, while remaining flexible enough to accommodate diverse life-history traits, varying numbers of life stages per species, and interaction patterns. As such, our approach is widely applicable to a broad range of ecological contexts. Population structure introduces mechanisms that can drastically influence stability and resilience [81]. Our results demonstrate that structures of interacting populations significantly reshape the boundaries of stability, offering new insights into the interplay of cross-stage dynamics and network complexity.

The main limitation of using our framework together with random matrices precisely lies in the parametrization of the structured community matrix. The effect of a change in abundance of the total population of one species on the fractional abundance of a particular stage of another is not straightforward to derive even when assuming a given interaction type between the species. For instance, we have considered that competitive adult-adult interactions have a negative impact on the total abundance of the species while adult-juvenile competition has a negative impact on the fractional abundance of juveniles. The rationale is that competitive pressure in adults can decrease fecundity or adult abundance (decreasing total species abundance) while competitive pressure in juveniles decreases both adult and juvenile abundance (so that the fractional abundance of juveniles relative to the total population also decreases). However, there may be other ways to characterize competitive pressure on adults and juveniles. Similarly, stage-structured interactions might display an inherent structure in the Jacobian matrix [19], which is not accounted for when using random matrices. In addition, our findings so far have dealt with randomly assembled communities and have not attempted to study the effect of the underlying interaction network structure. In natural systems, species interactions are not random, rather they are shaped by long-term co-adaptation and evolutionary pressures that influence both the types and strengths of inter-species relationships [82]. This structured interaction network, often characterized by specific patterns like nestedness [83] or modularity [84], likely interacts with population structure in ways that significantly influence community stability and resilience.

These limitations can be addressed with future research. The effect of different inter-stage interaction types (e.g. competitive adult-adult interactions) on the total population or fractional abundance of the stages can be analytically determined by considering specific functional forms for stage-structured population dynamics. The challenge lies in mapping the effect of different interaction types on the abundances of the stages to the effect on the abundances of the total population and fraction of stages. In addition, the nuance of ecological communities could be investigated in our framework by considering different network-generating mechanisms that further constrain the elements of the structured community matrix. Other future directions include incorporating additional dimensions of population heterogeneity, such as sex or behaviour, that also influence interactions within and between species [85] or extending the analysis to address transient dynamics [30] using pseudospectra [86]. We argue that these proposed future extensions will provide enhanced realism to the complex picture of community behaviour, allowing for the exploration of both long-term stability and transient dynamics, a critical feature in understanding ecosystems under perturbations [87]. Finally, validating structured community models with empirical data across diverse ecosystems remains paramount. A first step could be to investigate the typical patterns of inter- and intra-stage interactions in natural communities that favour stability. These efforts will prove key in advancing predictive ecological modelling and informing conservation strategies that support biodiversity and ecosystem function.

Outstanding questions

- Is there a general stability criterion for communities composed of structured populations? Can we found it analytically?

- How does population structure affect the feasibility of the equilibrium points of the model?

- How does population structure affect ecological communities beyond local asymptotic stability?

- How would stability be affected by increasing asymmetric relationships through the inclusion of other types of individual heterogeneity, such as sex, behavioral types, or individual quality?

- What is the role of different types of interactions and asymmetry in empirical ecological systems, especially considering their inherently open and dynamic nature?

- What is the effect of the coupling between population structure and the interaction structure (e.g., modularity) that arises from co-adapted communities?

Glossary

- **Community Matrix:** A matrix that measures the direct effect of the abundance of species j on the population growth rate of species i. Formally, it is the Jacobian of a system of differential equations describing the dynamics of population abundances in a community evaluated at a fixed point.

- **Complexity**: In the context of the complexity-stability debate, complexity was defined by May as $\sigma\sqrt{SC}$, where S is species richness, C is connectance (the probability that any two species will interact with each other) and σ is the standard deviation of the interaction strength.

- **Diversity:** In community ecology, diversity refers to the co-occurrence of different species (or genotypes) in a particular environment and their respective interactions.

- **Dynamical systems**: A mathematical framework used to describe the evolution of a system over time. It consists of a set of variables that represent the system's state and a set of rules or equations (often differential or difference equations) that determine how these variables change in time.

- **Eigenvalues:** An eigenvalue of a square matrix A is a scalar *lambda* such that $Av = \lambda v$ for some non-zero vector v.

- **Equilibrium point:** A point in the phase space of a dynamical system that does not change over time. Also known as fixed point.

- **Feasible equilibrium point:** A fixed point of a dynamical system in which all measured entities have positive values. In the case of population dynamics, a feasible equilibrium is a fixed point in which all species have positive population densities.

- **Jacobian matrix:** A matrix of all first order partial derivatives of a given function.

- **Life cycle:** The whole life history of an organism, usually depicted through a series of developmental stages in which an organism goes through during its lifespan (e.g. from zygote into a mature form where another zygote can be produced) .

- **Local asymptotic stability:** A fixed point is locally stable if all infinitesimal perturbations of the system dampen and eventually converge to the fixed point, and locally unstable if there exists an infinitesimal perturbation after which the system never returns to the equilibrium.

- **Ordinary Differential Equations:** A differential equation dependent on only a single independent variable.

- **Population structure:** The distribution of individuals of a population with respect to different attributes, such as age, developmental stage, size, sex, genetics, etc.

- **Pseudospectral analysis:** The ε pseudospectrum of a matrix $\boldsymbol{A}$ consists of all eigenvalues of matrices that are ε-close to $\boldsymbol{A}$. This is, the eigenvalues of $\boldsymbol{A}_\varepsilon = A + E$, where $\|E\| \leq \varepsilon$.

- **Random Matrix:** A matrix in which some or all of its entries are sampled randomly from a probability distribution.

- **Reactivity:** The maximum instantaneous growth rate of small perturbations to a system equilibrium.

- **Transient dynamics:** The evolution of a dynamical system following a perturbation or change, for example as it moves from one equilibrium state to another.

- **Vital rates:** Rates or probabilities of vital occurrences that affect changes in the size and composition of a population, e.g. survival, growth/development or reproduction.

Highlights

- We generalise the traditional community matrix to study community stability by incorporating population structure, accounting for interactions across life stages.

- Adult-juvenile predator-prey dynamics between species can stabilise communities that non-structured models predict to be unstable, while competitive adult-juvenile interactions are destabilising.

- Stage-specific interactions reveal new promising pathways to community resilience, bridging the gap between theoretical predictions of instability and empirical observations of stability in complex ecosystems.

- The structured community matrix offers a systematic method for assessing ecosystem stability, adaptable to various interaction types and ecological contexts.

- Our framework provides a road map for future research into the stability of structured populations, with potential applications in conservation and ecosystem management.

Acknowledgments

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Supplementary Information for

Population structure plays a key role in community stability

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1 Homogeneous interaction types

We begin by examining communities where all interactions—adult-adult, adult-juvenile, juvenile-adult, and juvenile-juvenile—are of the same type. These homogeneous configurations include four scenarios: all random, all mutualistic $(+/+)$, all competitive $(-/-)$, or all predator-prey interactions.

We parametrize the structured community matrix (SCM) considering the following criteria:

- If $i \neq j$
  - **Random interactions**:
    * $M_{ij}^1 \sim \mathcal{N}(0, \sigma_1)$ with probability C, 0 otherwise.
    * $M_{ij}^2 \sim \mathcal{N}(0, \sigma_2)$ with probability C, 0 otherwise.
    * $M_{ij}^3 \sim \mathcal{N}(0, \sigma_3)$ with probability C, 0 otherwise.
    * $M_{ij}^4 \sim \mathcal{N}(0, \sigma_4)$ with probability C, 0 otherwise.

    With $\gamma_i = \sigma_i \sqrt{SC}$.
  - **Mutualistic interactions**
    * $M_{ij}^1 \sim |\mathcal{N}(0, \sigma_1)|$ with probability C, 0 otherwise.
    * $M_{ij}^2 \sim |\mathcal{N}(0, \sigma_2)|$ with probability C, 0 otherwise.
    * $M_{ij}^3 \sim |\mathcal{N}(0, \sigma_3)|$ with probability C, 0 otherwise.
    * $M_{ij}^4 \sim |\mathcal{N}(0, \sigma_4)|$ with probability C, 0 otherwise.

    With $\gamma_i = \sigma_i C(S-1)\sqrt{\dfrac{2}{\pi}}$.
  - **Competitive interactions**
    * $M_{ij}^1 \sim -|\mathcal{N}(0, \sigma_1)|$ with probability C, 0 otherwise.
    * $M_{ij}^2 \sim -|\mathcal{N}(0, \sigma_2)|$ with probability C, 0 otherwise.
    * $M_{ij}^3 \sim -|\mathcal{N}(0, \sigma_3)|$ with probability C, 0 otherwise.

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$*$ $M_{ij}^4 \sim -|\mathcal{N}(0,\sigma_4)|$ with probability C, 0 otherwise.

With $\gamma_i = \sigma_i \left\{ \sqrt{SC} \left(1 + \dfrac{2-2C}{\pi-2C} \right) \sqrt{\dfrac{\pi-2C}{\pi}} + C\sqrt{\dfrac{2}{\pi}} \right\}$.

– **Predator-prey interactions**

With probability C each pair of species interact and with probability $1/2$ species i predates on j (otherwise j predates on i).

If species i predates on species j we consider (otherwise the sign relation is inverted):

$*$ $M_{ij}^1 \sim |\mathcal{N}(0,\sigma_1)|$ and $M_{ji}^1 = -|\mathcal{N}(0,\sigma_1)|$

$*$ $M_{ij}^2 \sim |\mathcal{N}(0,\sigma_2)|$ and $M_{ji}^2 = -|\mathcal{N}(0,\sigma_2)|$

$*$ $M_{ij}^3 \sim |\mathcal{N}(0,\sigma_3)|$ and $M_{ji}^3 = -|\mathcal{N}(0,\sigma_3)|$

$*$ $M_{ij}^4 \sim |\mathcal{N}(0,\sigma_4)|$ and $M_{ji}^4 = -|\mathcal{N}(0,\sigma_4)|$

With $\gamma_i = \dfrac{\pi-2}{\pi}\sigma_i\sqrt{SC}$.

- If $i = j$

  – $M_{ii}^1 = -d$

  – $M_{ii}^2 \sim \mathcal{N}(0,\sigma_2)$

 – $M_{ii}^3 \sim \mathcal{N}(0,\sigma_3)$

  – $M_{ii}^4 = -d$

Recall that these matrices represent:

- M_{ij}^1: change in growth rate of the total abundance of species i after a change in total abundance of species j

- M_{ij}^2: change in growth rate of the fraction of juveniles in species i after a change in total abundance of species j

- M_{ij}^3: change in growth rate of the total abundance of species i after a change in the abundance of juveniles of species j

- M_{ij}^4: change in growth rate of the fraction of species i after a change in the abundance of the fraction of juveniles of species j

In all our simulations we used $C = 1$, $\mu = 1$ and $S = 1000$. We used several values of γ (note that γ is a function of σ so that knowing the value of one the other is completely determined) as can be observed in the panels of Fig. 1.

In these cases, communities predicted as unstable by unstructured models remain unstable even when stage structure is introduced. However, if the strength of adult-juvenile (or juvenile-adult) interactions becomes sufficiently large, communities initially predicted as stable by unstructured models may become unstable Fig. 1(A-F).

Following from the general result of Rober May [1], it would be expected that the volume of the phase space with stable communities decreased when the interaction strength of total populations (γ_1) increases. Following from the general result of Rober May [1], one would expect that, as the interaction strength of total populations (γ_1) increases, the possible number of stable communities decreased. This is observed in the case of random (not shown), mutualistic and predator-prey interactions, but not for competitive ones. We observe an intermediate point at higher values of total population to total population interaction strength in which the number of possible stable communities is optimum Fig. 1(G).
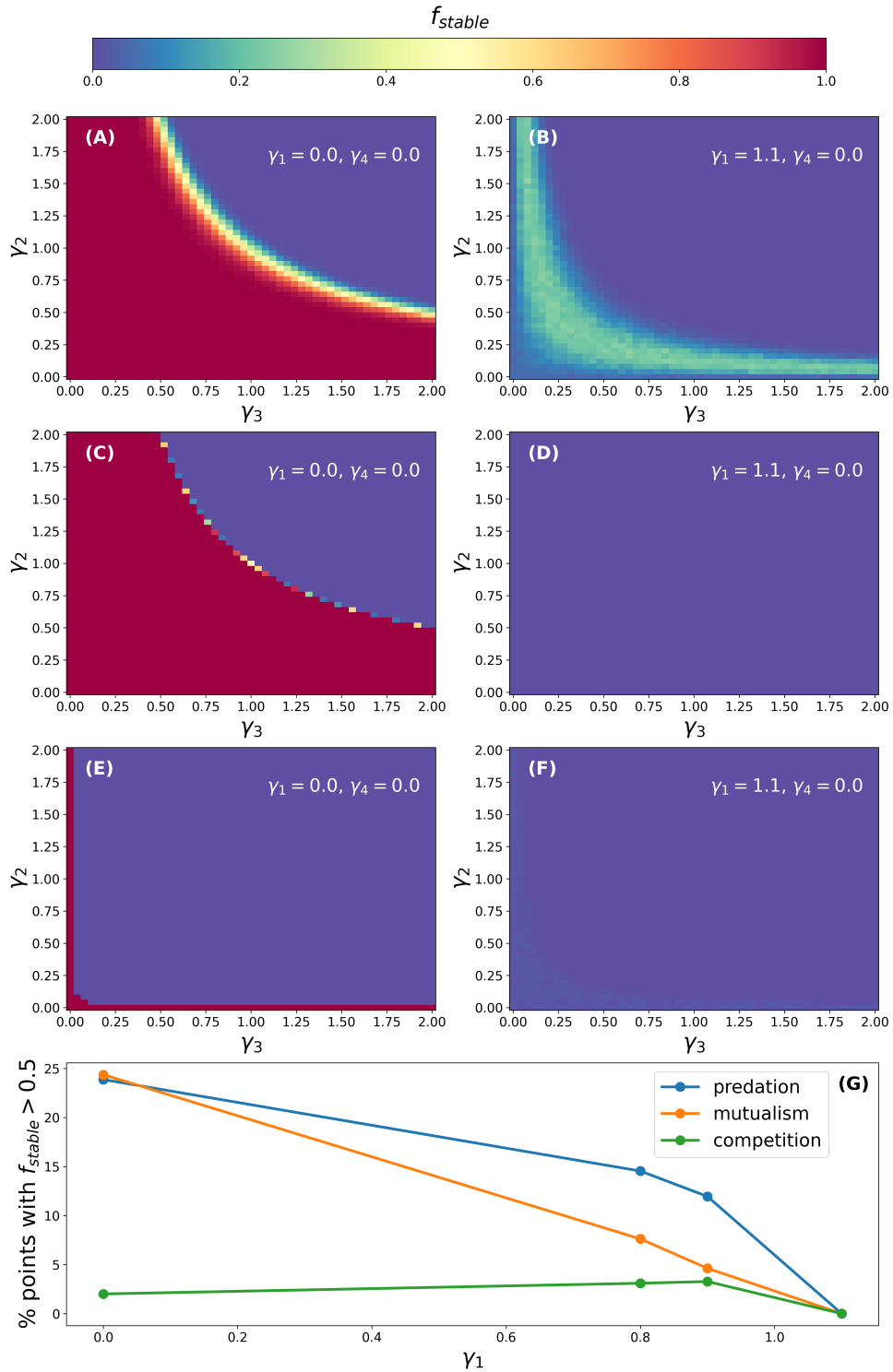
Figure 1: Stability analysis of communities with homogeneous random interactions. The proportion stable communities are shown for a case where all interaction types (adult-adult, adult-juvenile, juvenile-adult, and juvenile-juvenile) are (A-B) predator prey, (C-D) mutualistic, and (E-F) competitive. (G) Percentage of parameter combinations ((γ_2, γ_3), with respect of the total number of combinations explored) for which more than 50% of the simulated communities are stable.

2   Stage-symmetric interaction types

Adult-adult and juvenile-juvenile interactions are of the same type but different from the adult-juvenile and juvenile-adult interaction type. We switch off juvenile-juvenile interactions for simplicity.

The parametrization of the SCM follows the same rules as before, but now each matrix (M^1 to M^4) will display a different sign relation depending on the interaction type considered between stages. For instance, the parametrization of the SCM for a community with **adult-adult competition and adult-juvenile (and juvenile-adult) predator-prey interactions** would consist of the following rules:

- If $i \neq j$:
    - $M_{ij}^1 \sim -|\mathcal{N}(0, \sigma_1)|$
    - $M_{ij}^2 \sim |\mathcal{N}(0, \sigma_2)|$ and $M_{ji}^2 = -|\mathcal{N}(0, \sigma_2)|$ (if species i predates on species j, otherwise signs inverted)
    - $M_{ij}^3 \sim |\mathcal{N}(0, \sigma_3)|$ and $M_{ji}^3 = -|\mathcal{N}(0, \sigma_3)|$ (if species i predates on species j, otherwise signs inverted)
    - $M_{ij}^4 = 0$ (juvenile-juvenile interactions are not considered)
- If $i = j$:
    - $M_{ii}^1 = -d$
    - $M_{ii}^2 \sim \mathcal{N}(0, \sigma_2)$
   - $M_{ii}^3 \sim \mathcal{N}(0, \sigma_3)$
    - $M_{ii}^4 = -d$

Again, we consider $S = 1000$, $C = 1$ and $\mu = 1$ in all the simulations.

Adult-juvenile predator-prey interactions provide a stabilizing effect: communities predicted as **unstable** by unstructured population models can become **stable** when stage-structure is considered. This is independent of the adult-adult interaction type and occurs for intermediate values of the adult-juvenile interaction strength. For too low or to high values, the community is not stabilized. See Fig. 2.
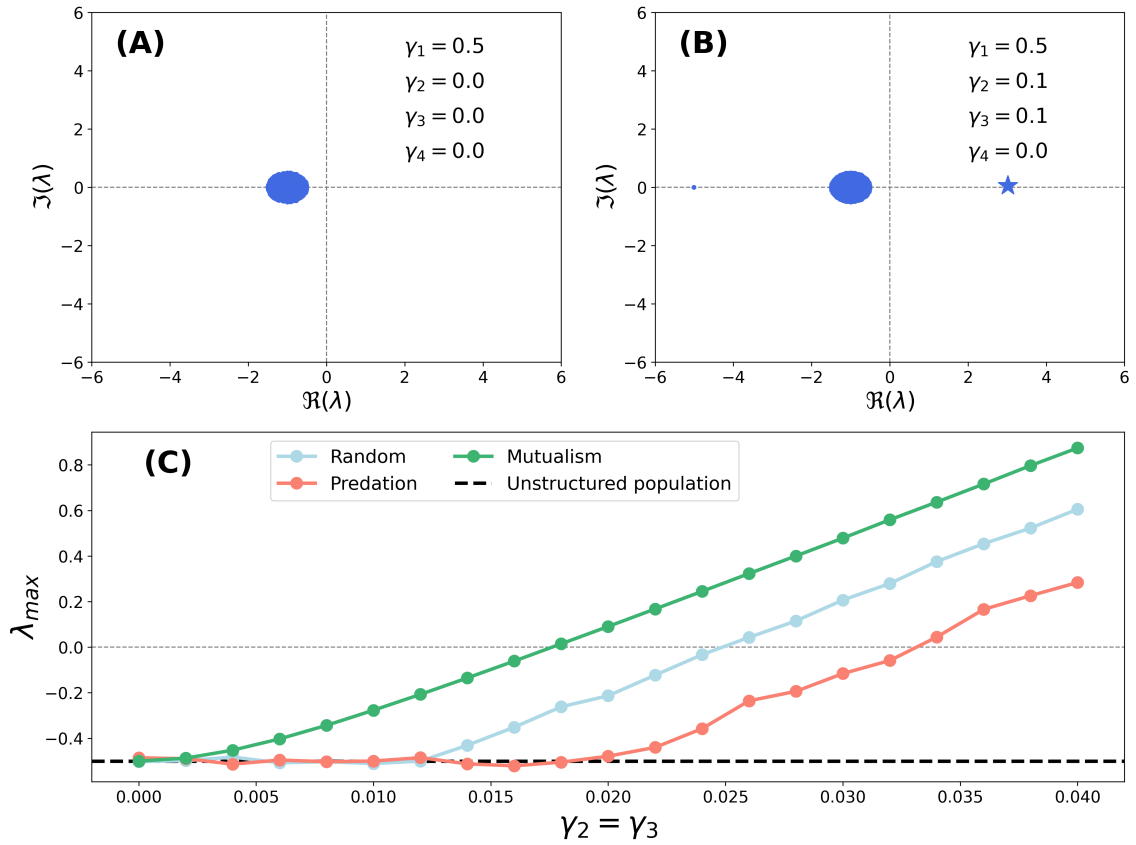
Competitive adult-juvenile interactions are destabilizing: communities predicted as **stable** by unstructured population models can become **unstable** when stage-structure is considered. This is independent of the adult-adult interaction type. See Fig. 3.

Mutualistic adult-juvenile interactions have a neutral effect: communities that would be predicted as **unstable** by unstructured population models keep being **unstable** when stage-structure is considered. Of course high values of adult-juvenile interaction strength can also destabilize a community, as previously shown. See Fig. 4.
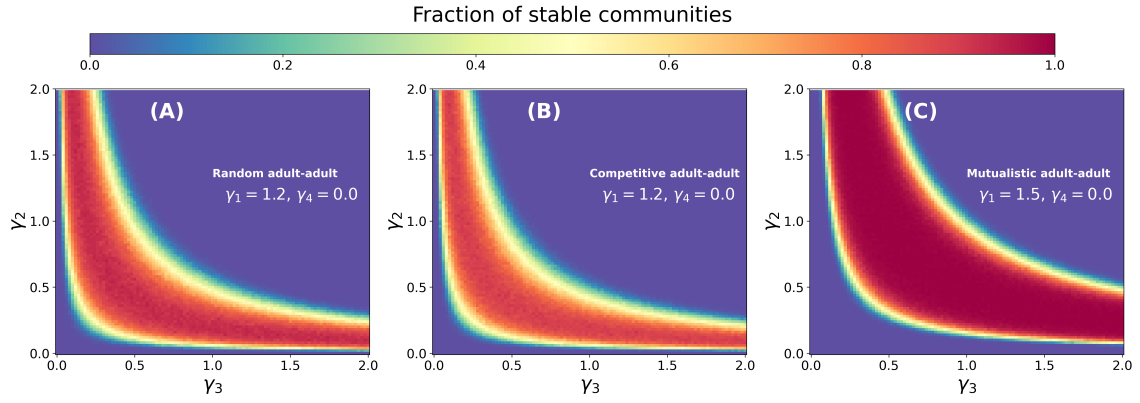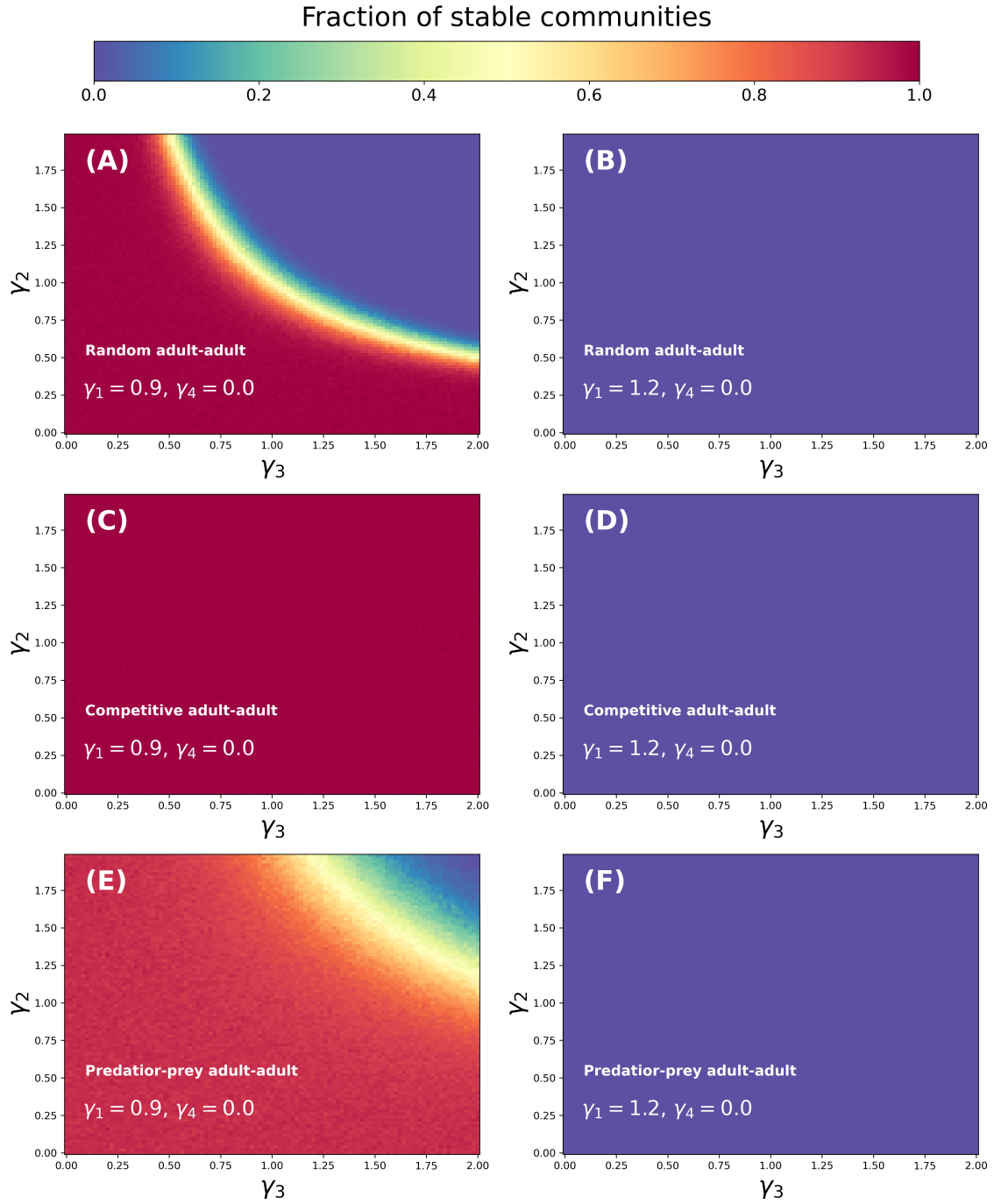
Figure 2: Stability analysis of communities with adult-juvenile predator-prey interactions. In all cases an unstructured population model would predict an unstable community ($\gamma_1 > 1$). We observe that intermediate values of adult-juvenile (γ_2) and juvenile-adult (γ_3) interaction strength promote community stability.

Figure 3: Stability analysis of communities with adult-juvenile competitive interactions.
(A) Eigenvalues of the structured community matrix with $\gamma_1 = 0.5$ and $\gamma_2 = \gamma_3 = \gamma_4 = 0.0$, so that essentially the adult-juvenile and juvenile-juvenile interactions are switched off. (B) Eigenvalues of the structured community matrix with $\gamma_1 = 0.5$, $\gamma_2 = \gamma_3 = 0.1$ and γ_4, so that adult-juvenile interactions are switched on with quite low interaction strength and juvenile-juvenile interactions are still deactivated. We observe that $\text{Re}\{\lambda_{max}\} > 0$, making the community unstable. (C) This behaviour is observed independently on the adult-adult interaction type, although the transition to instability occurs at different values of the juvenile-adult (and adult-juvenile) interaction strength, $\gamma_2 = \gamma_3$. In this case, an structured population model would predict that the community is stable, so that competitive adult-juvenile interactions are destabilizing.

Figure 4: Stability analysis of communities with adult-juvenile mutualistic interactions.
Each row corresponds to one type of adult-adult interaction: Random (A-B), competitive (C-D) and predator-prey (E-F). The first column corresponds to a case in which an unstructured population model would predict a stable community, while in the second it would predict an unstable one. Independently on the type of adult-adult interactions, mutualistic adult-juvenile interactions are not able to stabilise communities. On the other hand, if the adult-juvenile interaction strength is big enough, stable communities as predicted by unstructured population models can become unstable.