Check for updates

Received: 23 October 2023 | Revised: 11 March 2024 | Accepted: 13 March 2024

DOI: 10.1111/ele.14413

LETTER

ECOLOGY LETTERS cnrs WILEY

A taxonomy of multiple stable states in complex ecological communities

Guim Aguadé-Gorgorió[1] | Jean-François Arnoldi[2] | Matthieu Barbier[3] | Sonia Kéfi[1,4]

[1]ISEM, Univ Montpellier, CNRS, IRD, Montpellier, France

[2]Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier University, Moulis, France

[3]PHIM Plant Health Institute, University of Montpellier, CIRAD, INRAE, Institut Agro, IRD, Montpellier, France

[4]France Santa Fe Institute, Santa Fe, New Mexico, USA

Correspondence
Guim Aguadé-Gorgorió, Institut des Sciences de l'Évolution de Montpellier (ISEM), Université de Montpellier, Campus Triolet, Batiment 22, cc065, 34095 Montpellier Cedex 05, France.
Email: guimaguade@gmail.com

Funding information
Fundación Ramon Areces; French National Research Agency ANR, Grant/Award Number: ANR-18-CE02-0010-01

Editor: Po-Ju Ke

Abstract

Natural systems are built from multiple interconnected units, making their dynamics, functioning and fragility notoriously hard to predict. A fragility scenario of particular relevance concerns so-called regime shifts: abrupt transitions from healthy to degraded ecosystem states. An explanation for these shifts is that they arise as transitions between alternative stable states, a process that is well-understood in few-species models. However, how multistability upscales with system complexity remains a debated question. Here, we identify that four different multistability regimes generically emerge in models of species-rich communities and other archetypical complex biological systems assuming random interactions. Across the studied models, each regime consistently emerges under a specific interaction scheme and leaves a distinct set of fingerprints in terms of the number of observed states, their species richness and their response to perturbations. Our results help clarify the conditions and types of multistability that can be expected to occur in complex ecological communities.

KEYWORDS

community ecology, complex systems, multiple stable states, regime shifts

INTRODUCTION

Natural ecosystems are deteriorating at unprecedented rates, with climate change deeply altering their functioning and the services they provide to human societies. There is an urgent need to understand how ecosystems react to environmental changes, a task made difficult by the inherent complexity of communities of many interacting species. Of particular importance are ecosystems found to respond abruptly to gradual changes in environmental conditions (Petraitis, 2013; Rocha et al., 2015; Scheffer et al., 2001). Key examples of these so-called *catastrophic shifts* are the abrupt eutrophication of shallow lakes (Scheffer et al., 1993; Scheffer & Jeppesen, 2007), the desertification of arid ecosystems (Kéfi et al., 2007; Schlesinger et al., 1990), the bleaching of coral reefs (Graham et al., 2015) or the degradation of tropical forests into treeless landscapes (Hirota et al., 2011). The occurrence of abrupt transitions suggests that some ecosystems can exist in multiple stable states within a range of environmental conditions. Small perturbations could then induce transitions between those states, leading to large shifts from species-rich communities towards degraded ecosystem states.

The possibility that dynamical systems can be multistable and undergo abrupt shifts is also relevant across a variety of research fields (Scheffer, 2020): Sharp shifts have been reported in the human gut microbiome (Lozupone et al., 2012), in neuronal activity in the brain (Litt et al., 2001) or even in financial markets (May

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.
© 2024 The Authors. *Ecology Letters* published by John Wiley & Sons Ltd.

et al., 2008), all of which are characterized by a complex architecture of many interacting elements. Uncovering what mechanisms make these systems multistable is a key step towards predicting their fragility.

In ecology in particular, the mechanisms generating multistability have been thoroughly described in single- or few-species dynamical models that do not always capture the complexity of species-rich communities (Kéfi et al., 2022; Kéfi, Holmgren, et al., 2016; Solé, 2011). Our current understanding of *tipping points*, therefore, largely ignores the role of species diversity and the complexity of their network of interactions (Beisner et al., 2003; Kéfi, Holmgren, et al., 2016; Scheffer et al., 2001, 2012). Why, and how, multiple stable states can emerge in species-rich ecosystems remain largely open questions (Figure 1a; Kéfi et al., 2022).

Recent research has uncovered specific scenarios in which multiple fixed points do emerge in species-rich models (Bunin, 2017; Fried et al., 2016; Gao et al., 2016; Kessler & Shnerb, 2015; Lever et al., 2014). Theoretical studies focusing on mutualistic systems, i.e. assuming only positive interactions between species, have identified the emergence of system-wide bistability arising from obligate and nonlinear cooperation (Gao et al., 2016; Laurence et al., 2019). Another large body of research is unveiling a very different scenario, where heterogeneous competition can engender many similar community states (Bunin, 2017; Diederich & Opper, 1989; Fried et al., 2016; Kessler & Shnerb, 2015; Supporting Information II.F, III.A for an overview of the literature). Beyond theoretical advances, species-rich multistability has also been recently described in experimental microbial communities (Amor et al., 2020; Fujita et al., 2023; Lopes et al., 2023).

The majority of these results, however, investigate the emergence of multistability in a single model or under a specific interaction scheme. How these isolated observations are connected, if other regimes exist and how to detect them empirically remains unclear: we lack a general common framework to describe the emergence of multistability in complex, species-rich ecosystems. This framework should accommodate the above multistability observations and propose how each could be detected in natural systems.

In the present work, we analyse the emergence of multistability across complex biological models. We focus on a mathematical model of a community in which many species interact through cooperation and competition. We first analyse a limit-case scenario in which all species are inherently bistable, with population dynamics characterized by an Allee Effect that limits their growth at low density (Courchamp et al., 2008). We then compare the outcomes of these analyses with those of other models where species can only reach a single stable state when alone. This allows us to investigate if multistability in complex communities emerges only from bistability at the level of species, or if community level processes also play a role of their own (Figure 1a). We also extend our analysis to multiple interaction types and other biological models, which enable us to assess the generality of our findings.

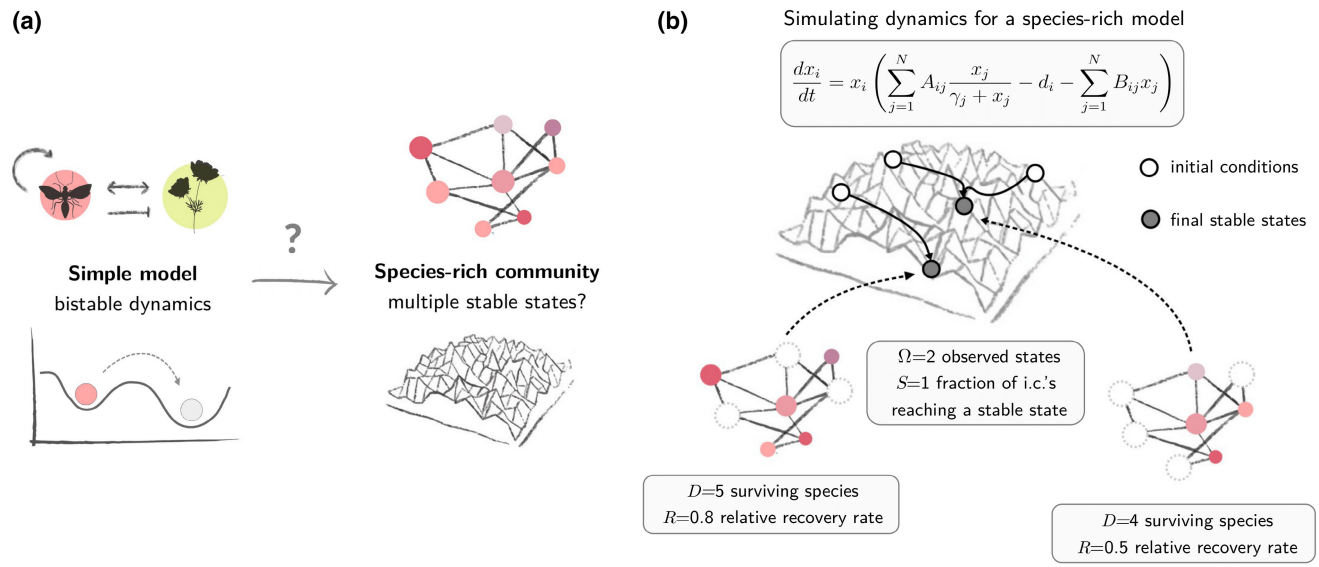

FIGURE 1 Scaling up low-dimensional bistability to the community level. (a) Our understanding of abrupt transitions in ecosystems mostly relies on simple models that do not take into account the role of species diversity. The stable states of such models can be visualized through the stability landscape: the relation between a system state variable x (horizontal axes) and a potential landscape $V = -S$, where S provides a metric of system stability (vertical axis). In few-species models, stability landscapes are often simple, with the system falling in one of the few possible stable states (valleys in the landscape). In higher-dimensional systems, however, stability landscapes are far from trivial: they can be very rugged, contain many stable states and are often impossible to quantify with a single metric V. (b) Here, we study the emergence of multistability in species-rich community models and across complex systems. To do so, we explore multiple models and interaction types and obtain, for each, a set of multistability properties such as the fraction of simulations reaching a stable state S, the number of observed stable states Ω, the species richness of these states D and the likelihood that they recover from perturbations R.

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Our aim is to bridge the gap between low-dimensional theory and empirical species-rich observations. To do so, we characterize different multistability regimes, their emergence across high-dimensional models and their relation to empirical patterns. Our work provides a simple taxonomy to classify the types of multistability that a species-rich model can display and reveals that the same four multistability regimes and their signatures consistently emerge across models of complex systems.

METHODS

A species-rich community of bistable species

We study a community model where each of N species is subject to an Allee Effect (Courchamp et al., 2008). Let x_i be the abundance of species i, with $i \in 1, 2, \ldots, N$. The temporal dynamics of each species follows:

$$\frac{dx_i}{dt} = x_i\left(\sum_{j=1}^{N} A_{ij}\frac{x_j}{\gamma_j + x_j} - d_i - \sum_{j=1}^{N} B_{ij}x_j\right), \quad (1)$$

where all parameters are positive. Here, A_{ii} is the maximum growth rate of species i when isolated, and B_{ii} determines the strength of self-regulation. Mutualism is included by considering that the abundance of species j can increase the growth rate of species i, saturating at a maximum value A_{ij} (Wright, 1989). Saturation follows a Holling type II functional response, reflecting the fact that species at high population abundances no longer increase their mutual benefits (Holland et al., 2002; Rohr et al., 2014; Supporting Information II.A). The parameter γ_j reflects the amount of j-individuals necessary to achieve half of the maximum contribution to growth rates (Wright, 1989). Conversely, the matrix elements $B_{ij} > 0$ determine the negative effect of species j on species i due to competition for space or resources (Chase et al., 2002).

Species-specific parameters are generated as positive random values from log-normal distributions (Supporting Information I.C). Mean values of the underlying normal distributions are set to $\langle d_i \rangle = 0.1$, $\langle \gamma_i \rangle = 1.0$, $\langle A_{ii} \rangle = 0.5$ and $\langle B_{ii} \rangle = 0.1$ and $\sigma = 0.1$ (Supporting Information I.C). The central results of this work are, however, not specific to these values. Parameter changes, and even different models (see below and Supporting Information III), only modify the location of each regime, but not its properties (Supporting Information I.C.2–3; see Adler et al., 2018; Fort, 2018; Spaak et al., 2021 for research on community model parameterization).

Building a multi-interaction network

Species interactions in the studied model are separated into cooperative (A) and competitive (B) matrices. In some interactions, such as facilitation and competition between plants, it may be empirically difficult to assess each process individually, in which case only the net effect between species can be used to parameterize a single interaction matrix (Laska & Wootton, 1998). However, separating interaction types into different network layers provides a powerful mathematical framework to understand complex ecological systems such as plant-pollinator communities (Lever et al., 2014; Pilosof et al., 2017; Rohr et al., 2014). Indeed, it has been shown that incorporating the multiple interaction types that occur in natural communities into ecological models can fundamentally affect our understanding of ecosystem dynamics and resilience (Kéfi, Miele, et al., 2016; Mougi & Kondoh, 2012).

Moreover, multiple interaction types can even happen simultaneously between a single pair of species. For example, some species can first recruit another ($A_{ij} > 0$), which can then later in life become a competitor ($B_{ij} > 0$), as seen in algae-mussel interactions (Kéfi, Miele, et al., 2016; Wieters, 2005). In drylands, annual plants can significantly improve water status locally, while at the same time competing with shrubs for this limited resource (Holzapfel & Mahall, 1999). To explore these diverse scenarios, we first allow species pairs to interact only through cooperation or competition, and later study the scenarios emerging when both interactions can occur simultaneously. Finally, we study other models where interactions are restricted to a single matrix A and find the same qualitative results (see below and Supporting Information III).

To implement this, matrices A and B are built independently and have randomly distributed interaction strengths. This provides a simple method to explore a large space of possible interaction scenarios with minimal assumptions (Supporting Information I.C; Barbier et al., 2018; May, 1972). An interaction between species i and j exists with probability p; otherwise $A_{ij} = 0$ or $B_{ij} = 0$ with probability $(1 - p)$ (Erdös-Rényi graphs, Supporting Information I.C.4, II.F.3). We sample a wide range of interaction strengths, where for example interspecific competition can be weaker or stronger than self-regulation (Adler et al., 2018; Barabás et al., 2016; Hu et al., 2022) and where the relative strengths of cooperation and competition can be tuned (Lopes et al., 2023). We explore the effect of varying the means (Figures 2a,b and 3; $A_{ij} \in [0, A_{ii}]$, $B_{ij} \in [0, 2B_{ii}]$), standard deviation (Figure 2c; $\sigma \in [0,2.0]$) and connectivity (Supporting Information II.F.3; $p \in [0, 1]$) of interactions, while predatory interactions are studied in Supporting Information II.D.

Numerical and mathematical analysis

To find stable states in the system of Equation (1), we numerically solve it with a Runge–Kutta method of order

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

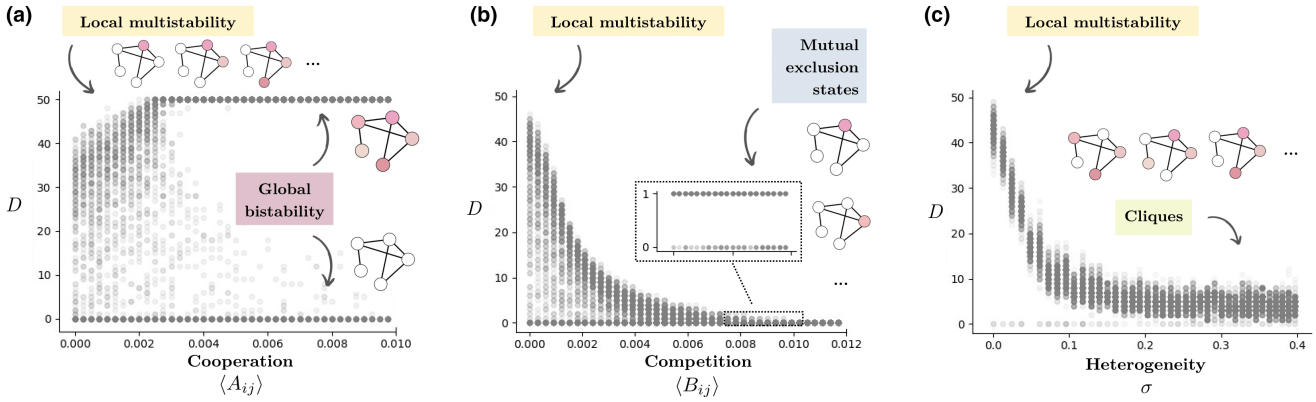

FIGURE 2 Multiple stable states under increasing mutualism, competition and interaction heterogeneity. We explore how local multistability, resulting from independent bistable species, upscales under increasing mutualism (a), competition (b) and interaction heterogeneity (c). Each grey dot represents the final diversity (D, number of surviving species) of a simulation starting from random initial conditions and $N = 50$ species (200 random initial conditions are generated for each value of the x axis). (a) Under increasing mutualism and no competition ($B_{ij} = 0 \, \forall \, i \neq j$), the 2^N states of independent species bistability upscale towards an all-or-nothing bistable regime. (b) Competition in the absence of mutualism ($A_{ij} = 0 \, \forall \, i \neq j$) reduces the amount of species that can survive in these local states, until we see N states, each with only one species surviving. (c) Under heterogeneous interactions, the system attains a region with many stable states, but all with similar diversity. We consider low heterogeneity ($\sigma = 0.05$) for (a) and (b), and weak interactions ($\langle A_{ij} = 0.25, \langle B_{ij} \rangle = 0.1$) for (c).

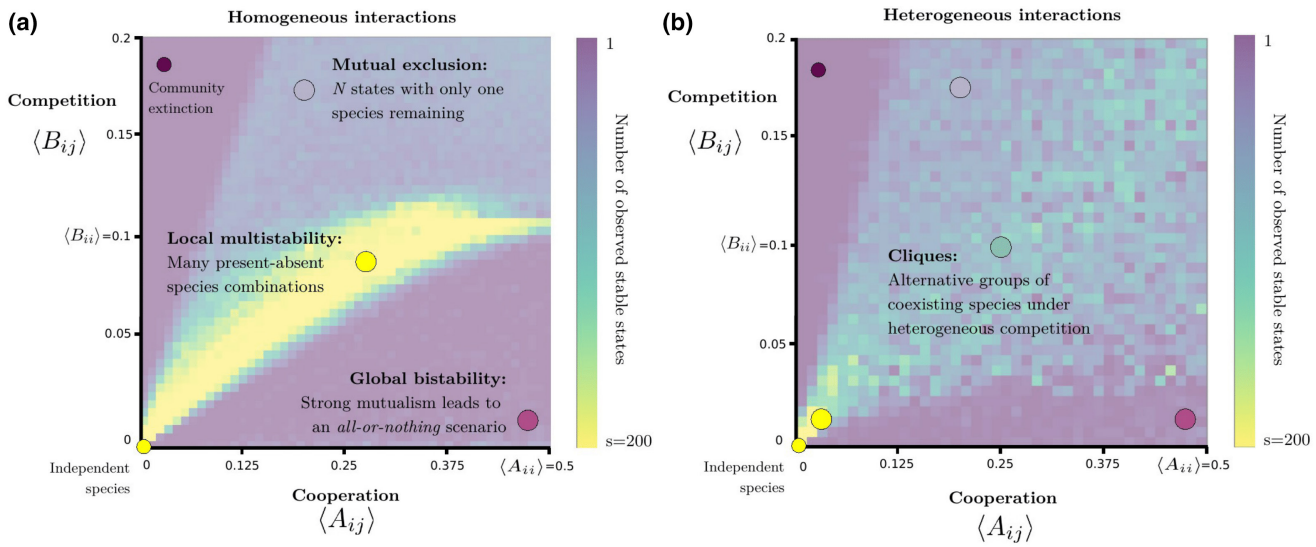

FIGURE 3 Emergence of four multistability regimes in ecological communities: Number of stable states (Ω, colour scale) observed after $s = 200$ simulations with random initial conditions, for homogeneous (a) and heterogeneous (b) interaction strengths and communities starting at $N = 50$ species. Highly-mutualistic systems show a global bistability pattern ($\Omega \sim 2$) emerging from single-species bistabilities. At the other extreme, strong competition generates mutual exclusion states as well as community extinction ($\Omega \sim N + 1$). In between these, single-species bistabilities can generate a high multiplicity of local states ($\Omega > > N$). Heterogeneous interactions (b) generate a fourth multistability regime characterized by many states with similar biomass and diversity. Interestingly, both local multistability and cliques emerge in regions involving both cooperation and competition and harbour many stable states: we might need additional information to distinguish between one or the other regime (Box 1). The coloured dots illustrate where each regime is located.

5(4) (Dormand & Prince, 1980). We define a system by setting intraspecific and interspecific interaction strengths and run $s = 200$ simulations for Figures 2–4 and $s = 10^4$ for Figure 4b. For each simulation, we generate random initial conditions with species abundances $x_i(t = 0)$ ranging from zero to values twice the individual Allee Effect thresholds, so that species initially start below or above their survival threshold with no preferred configuration (Supporting Information I.C). We simulate the dynamics during a fixed time of $t = 10^4$ timesteps (Supporting Information I.D.1), and store the final state of the system (Supporting Information I.D).

To evaluate if the final state is stable, we integrate the dynamics for $t = 10^2$ additional timesteps and check if all species abundances before and after the added time are equivalent. (Supporting Information II.E.2, II.F.2). We also check if the state is stable to species invasions. If not, it could mean that it appears stable only because potential invaders have gone extinct (Supporting Information II.F.2; Roy et al., 2020). To avoid this, we

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

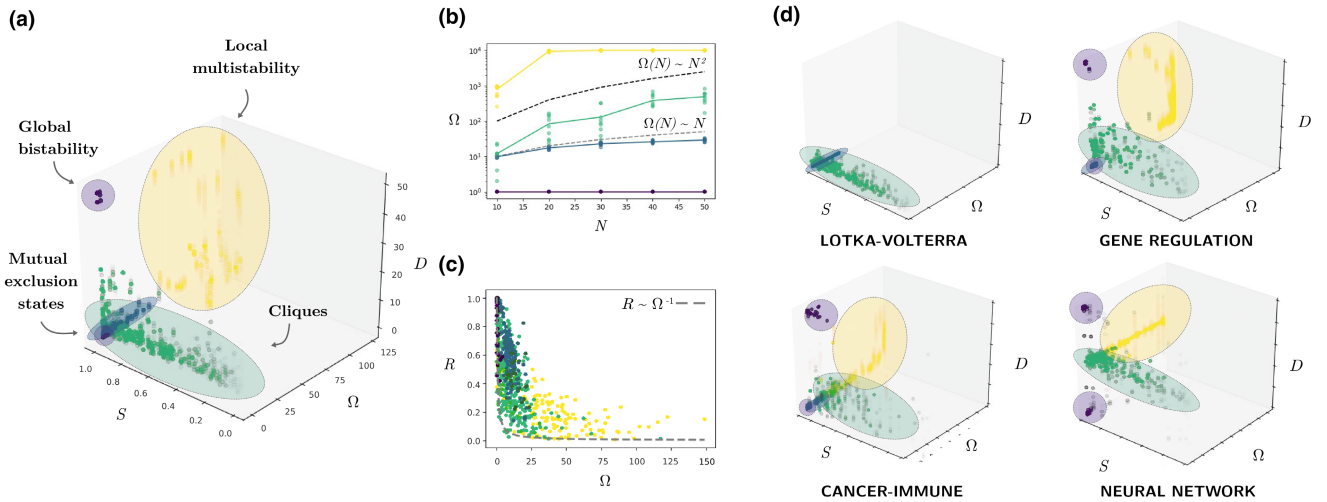

FIGURE 4 Identifying distinct fingerprints of the multistability regimes. Here we analyse the signatures of each multistability regime using simple measurable metrics. (a) We generate 300 systems with random $\langle A \rangle, \langle B \rangle, \sigma$ values and $N = 50$. For each system, we run $s = 200$ simulations starting from random initial conditions (Supporting Information I). Each dot of the figure represents the final properties of a simulation for a given system and initial conditions (300 × 200 dots), and is plotted with high transparency so that opaque areas show where most dots overlap. Each dot reflects the number of surviving species D in a final state, the number of states Ω and the fraction of stable runs S observed. Note that D is a property that can change for each of the 200 simulations in a system, while Ω and S are aggregated properties of the system across initial conditions. Each multistability family seats within a well-defined cluster. Colours are chosen by measuring in which of the four domains of Figure 3 the random $\langle A \rangle, \langle B \rangle, \sigma$ fall (Supporting Information II.G.4), while coloured circles around clusters are drawn at hand to improve visualization. (b) Scaling of the number of observed states Ω with species number N, with N ranging from 10 to 50. We generate up to $s = 10^4$ initial conditions to ensure that we explore a large number of possible stable states Ω. There are still many more local multistability states than simulations as $2^N > 10^4$, which explains the asymptote in the yellow line. The $\Omega = 2^N$ fit is tested for smaller community sizes in Supporting Information II.G.1. (c) We also test stable states against random perturbations of variable magnitude (Δx_i, Supporting Information I.E) and count the fraction of times the same state is recovered as a proxy for *basin stability*. Our tests show a lower resilience bound at $R \sim \Omega^{-1}$ (dashed line): the basin stability of stable communities rapidly decays when they are surrounded by a multiplicity of other states. (d) Qualitatively similar fingerprints are found for different complex systems: Generalized Lotka-Volterra communities (GLV), gene regulatory networks (GRN), cancer-immune interactions and random neural networks (Supporting Information III). The fact that not all regimes emerge in all models is consistent with the proposed taxonomy (see Equivalent Multistability Regimes and Fingerprints Across Complex Systems section).

avoid extinctions by setting a minimal threshold of $x_m = 10^{-10}$ beyond which the abundance of a species cannot keep decreasing (Supporting Information I.D.1).

Numerical simulations are described in further detail in Supporting Information I, and Python codes are available at https://github.com/GuimAguade/A-taxonomy-of-MSS-in-complex-ecological-communities. Complementary analytical techniques that support our results are discussed in Supporting Information II.A–C, II.E–G and III.

Measuring and classifying multistability properties

Once a stable state is found, we compare it to each state that was previously found for the same system (a set of equations with fixed parameters) but different initial conditions (Supporting Information I.D.2). For each system, we end up with a list of different observed states, allowing us to measure its multistability fingerprints (additional fingerprints are explored in II.G): (1) the fraction of initial conditions that reach a stable state without fluctuations (S) (Beninca et al., 2008; Hu et al., 2022); (2) the number of observed stable states (Ω), and (3) for each of the states in the list, its diversity of surviving species (D). Each system is thereby characterized by an Ω and an S value and as many D values as observed states. We generate systems with random interaction strengths, and we plot their multistability fingerprints in the three-dimensional space of possible (S, Ω, D) values (Figure 4a). Each dot is assigned a colour by classifying it into one of the four regimes identified (Supporting Information II.G.4).

We also study (4) how Ω and D scale with the number of species N (Figure 4b; Supporting Information II.G.1–2; Wright et al., 2021), and (5) if states recover after perturbations (Relman, 2012) (Supporting Information I.E). For this, we perturb stable states with normally distributed abundance changes Δx_i, and compute how often they recover their original species composition (R). This allows us to measure the basin of attraction of stable states and their relative stability (Menck et al., 2013) (Figure 4c; Supporting Information II.G.3).

Exploring the space of possible interaction schemes

We explore how different interaction schemes modulate the emergence and properties of stable states. Because

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

interaction types are segregated into two different network layers (Pilosof et al., 2017), we can investigate the individual effects of each interaction separately. We first study multistability in the absence of species interactions ($A_{ij} = B_{ij} = 0$ if $i \neq j$) and later explore the states that emerge under relatively homogeneous mutualism, competition and their combination (i.e. $\sigma \leq 0.1$; Supporting Information I.C, II.D–F). Finally, we explore the effects of increasing the heterogeneity of interaction strengths and network connectivity (Supporting Information II.F.3).

Other complex biological models

We replicate the above analysis on four archetypical models of complex biological systems, namely Lotka-Volterra interactions (Bunin, 2017), the cancer-immune interplay (Garay & Lefever, 1978), gene regulatory networks (Karlebach & Shamir, 2008) and neural cluster interactions in the brain (Stern et al., 2014; Supporting Information III). The generalized Lotka-Volterra model is of particular interest, as it describes a similar community as that of Equation (1) but without an Allee Effect. This allows us to assess if multistability at the community scale only emerges when species themselves are bistable. A detailed analysis of each model is presented in Supporting Information III, while their multistability fingerprints are displayed in Figure 4d.

RESULTS

For extremely weak interactions (i.e. $A_{ij} \approx B_{ij} \approx 0$ for $i \neq j$), species i can be either present ($x_i^* > 0$) or extinct ($x_i^* = 0$), depending on whether the initial abundance $x_i(t = 0)$ falls below or above an Allee Effect threshold (Supporting Information II.A; Courchamp et al., 2008). The community can then be in any of 2^N stable states, encompassing all possible combinations of *local* species presence and absence (Supporting Information II.A). We investigate below how this multistability landscape is affected by different interaction types.

Global and local stable states in mutualistic communities

Provided that cooperation strengths are strongly homogeneous, interspecies competition is held at zero and species connectivity is high ($A_{ij} \approx \langle A \rangle \, \forall i \neq j$, $B_{ij} = 0$ $\forall i \neq j$, $p \approx 1$; Supporting Information II.B, II.F.3), analytical and numerical results predict that communities can become bistable, such that all species either coexist or go extinct simultaneously (Figure 2a right; Supporting Information II.B; Gao et al., 2016; Tu et al., 2017). This happens in a parameter range where species do not survive if alone ($x_i^* = 0$ if $A_{ij} \approx 0$; Supporting Information II.A) and cooperation is strong enough. The community then collectively reproduces the bistable dynamics of each species: no species will survive unless cooperation is strong enough and the total initial abundance overcomes a predictable tipping point (Supporting Information II.B.1; Gao et al., 2016), above which all species survive together through a community level niche facilitation process (Figure 2a right; Koffel et al., 2021). This indicates that *global bistability* can emerge in systems where bistable species cooperate strongly as previously proposed in (Gao et al., 2016).

However, this perfect all-or-nothing regime breaks if some species can survive without the need for cooperation with others and interactions are relatively weak (Supporting Information II.B.2). Here, many *local multistability* states can emerge where only some species are present (Figure 2a left). This scenario becomes particularly relevant close to the tipping point of the globally bistable system. Here, the abrupt extinction of the whole community becomes blurred by many intermediate states, each involving gradually fewer species (Supporting Information II.B.2, II.G).

Local and mutual exclusion states in competitive communities

In Figure 2b we maintain the above homogeneity constraints on parameters, interactions and connectivity, and gradually increase the strength of competition $\langle B_{ij} \rangle$ ($A_{ij} = 0$ for $i \neq j$). Under very weak competition, the community can be again in many species presence-absence states (Figure 2b left). As competition increases, the number of species that can coexist decreases as expected (Arnoldi et al., 2016; Levin, 1970). However, local bistabilities can still generate many stable states: stronger competitors can be present or absent, hence excluding (or not) weaker species. The community can still be in many local states, with their multiplicity bounded by competition strength (Figure 2b middle; Supporting Information II.C).

Under stronger competition, we recover the well-known scenario of *mutual exclusion* (Petraitis, 2013): there exist N states with only one surviving competitor each (Figure 2b box). Under the Allee Effects and even stronger competition, only the global extinction state prevails. All competitors are pushed below their Allee Effect threshold and no species survive (Figure 2b bottom right; Supporting Information II.C.3; Wang et al., 1999).

Different multistability regimes under mixed interactions

Ecological communities are usually built on a varying mixture of positive and negative interspecies effects (Kéfi,

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

BOX 1 Distinguishing multistability regimes in empirical data—A simulated case study

Of the four multistability regimes, global bistability and mutual exclusion represent limit-case scenarios: dominant nonlinear cooperation generates an *all-or-none* regime (i.e. 'global bistability'), while extreme competition drives a *one-survives* signature (i.e. 'mutual exclusion'; Figure 4a). These rare fingerprints are unlikely to be found in any but experimentally engineered ecosystems. Instead, local multistability and clique regimes correspond to more nuanced scenarios. They are both characterized by a high multiplicity of stable states and emerge at intermediate mixtures of cooperation and competition (Figure 3). In many empirical scenarios, however, we might not be able to observe and characterize many replicas of a system and their properties (Schröder et al., 2005). Instead, we might only have temporal data for community composition (Gajer et al., 2012) or responses after a manipulation (Friman et al., 2015; Mehner et al., 2002). This means that the number of states (Figure 4b) or the interaction matrices (Figure 3) might not be accessible metrics to indicate what regime is at play, while diversity alone might not allow us to tell cliques and local states apart.

Here, we showcase a simulated experimental scenario in which we have time series data of species richness in an ecosystem. The system shows evidence of multistability in the form of community shifts after species extinctions (see e.g. Schröder et al., 2005 for a detailed analysis on multistability identification), and we want to know what multistability regime explains such shifts. Suppose that we have minimal knowledge of our system. We cannot infer $\langle A \rangle$, $\langle B \rangle$ nor σ, and only know that there might be cooperative and competitive interactions at play and that we cannot assume either of them to dominate. We also do not have information of the size of the species pool N and cannot follow the trajectories of all species, but just count their diversity or the abundance of one or two tracked species before and after a manipulation. One manipulation that can performed in certain systems is the local extinction of a given species (Supporting Information I.E). Albeit not always feasible and often requiring ethical assessment, selective extinctions can be done in spatially enclosed systems such as in lake experiments (Mehner et al., 2002) or in the lab, for example for given antibiotic sensitivities in microbial communities (Friman et al., 2015). For illustrative purposes, suppose that we can follow and perturb two different species while measuring the changes in diversity of the community before and after each manipulation (Figure 5).

Even in this minimal case study, our taxonomy can shed light on identifying the multistability regime at play. In local multistability, the extinction of a species happens if it goes below its Allee Effect threshold, showing that we do not even need to fully eradicate the species to drive it to extinction (Figure 5a; Supporting Information II.A). Furthermore, weak interactions indicate that no other species should react to the perturbation that the first extinction generates, and we would not observe secondary extinctions or invasions (Figure 5a purple). The shift in diversity should therefore be limited to $\Delta D = -1$ Instead, species survival in cliques is strongly intertwined: extinction of a species can alter the populations of others, driving secondary extinctions and invasions and potentially leading to a new community (Figure 5b). Therefore, ΔD can take values different from -1 (Supporting Information II.G.2). In the simulated experiment, even after we know that a tracked species has gone extinct and diversity should decrease by one, our measurement of $\Delta D = 0$ indicates that a new species has invaded (Figure 5b). Additional information of other species abundances would in fact show that a whole new community is in place, but the response of diversity alone can already indicate which multistability regime is behind observations.

Miele, et al., 2016; Mougi & Kondoh, 2012). To account for this, we keep the same constraints on interaction strength homogeneity $\sigma < 0.2$ and network connectivity $p \approx 1$, and explore systems with different mutualistic ($\langle A \rangle$) and competitive ($\langle B \rangle$) strengths (Figure 3a). For each system, we simulate the dynamics $s = 200$ times with random initial conditions (Supporting Information I.D), and count the number of observed stable states Ω.

Global bistability arises under dominant mutualism, so that the community exists in two stable states (Figure 3 purple). At the other extreme, strong competition generates N mutual exclusion states (Figure 3 blue), each with only one surviving species, and community extinction at even stronger $\langle B_{ij} \rangle$ (Figure 3 top left). Under mixed interactions, the two domains are separated by a highly multistable region that can be related to local multistability (Figure 3 yellow, Box 1). These states arise when the effects of mutualism and competition are balanced out, making each species locally bistable and allowing for a large number of species presence-absence combinations (Supporting Information II.E.1).

Emerging cliques under heterogeneous interactions

The previous results are valid when interaction strengths and connectivity are relatively uniform across

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

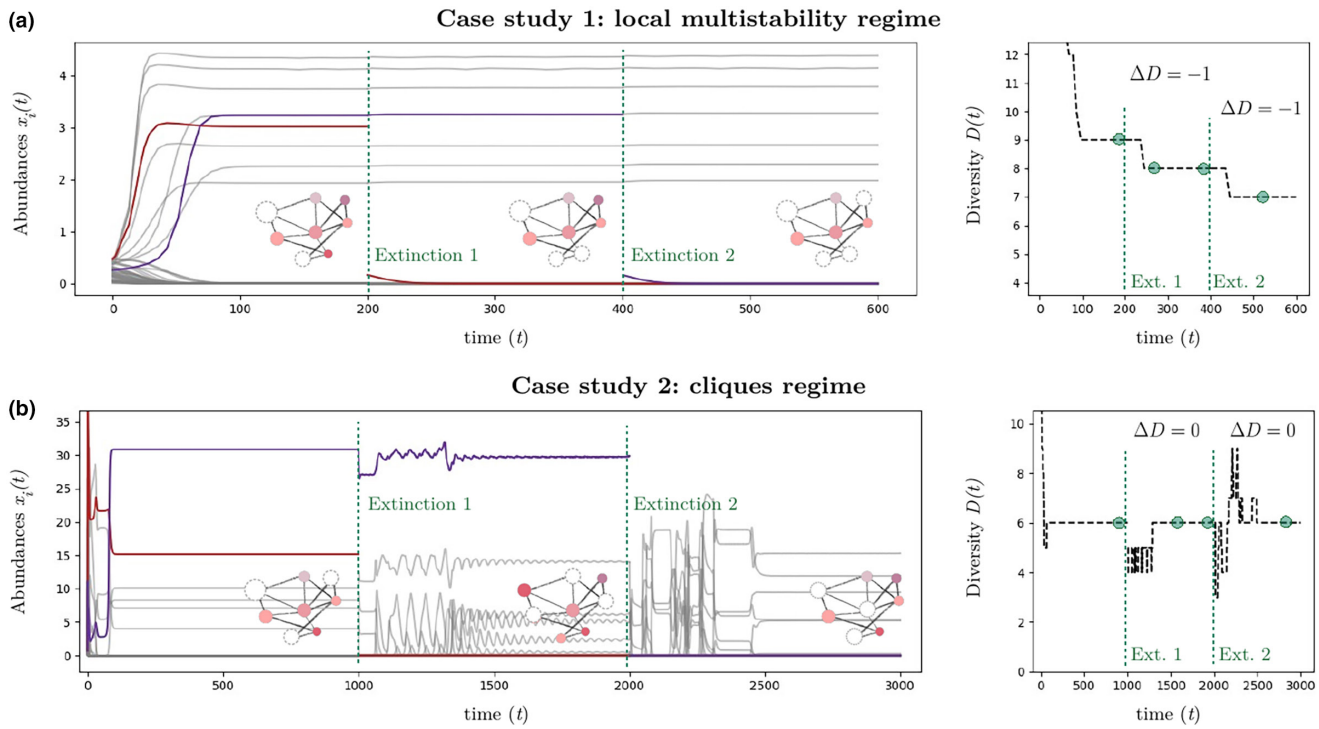

FIGURE 5 Distinguishing between multistability regimes. Here we show two minimal simulated case studies of multistability experiments as described in Box 1. We start with a community of $N = 50$ species that achieves a stable state, and we perturb it by extinguishing two species (red and purple) at two different time steps (green dashed lines). Knowledge on species trajectories (left panels) and community compositions (simplified network diagrams) or A and B values would allow us to accurately assess the multistability fingerprints in place. In realistic settings, however, we might only have access to much simpler data, such as community diversity (green circles, right panels) or the abundance of another species before and after a perturbation (red and purple lines) and A and B are tipically unknown. The $\Delta D = -1$ signature indicates only the tracked species has gone extinct with no other species reacting to it (local multistability, a). Any other ΔD signature would indicate that additional extinctions or invasions have happened. Because cliques often have different species compositions but the same diversity, the $\Delta D = 0$ signature tells us that, after the tracked species has gone extinct, others have invaded replacing the original community (b) The two systems have $\langle A \rangle = 0.25$ and $\langle B \rangle = 0.08$, but $\sigma = 0.06$ (a) and $\sigma = 0.6$ (b).

species (Supporting Information I). Ecological communities, however, often exhibit heterogeneous interactions (Bascompte, 2007; De Ruiter et al., 1995). As we increase the standard deviation of interaction strengths, our model captures the emergence of another multistability domain, which takes over a large proportion of the phase space (Figure 3b).

This regime is characterized by a high number of states, falling between the N states of mutual exclusion and the 2^N of local multistability (Figure 3; Supporting Information II.G.1). Beyond the number of states Ω, cliques can be differentiated from other regimes because they have consistently low species diversity (Figure 2c; Supporting Information II.F, III), show a characteristic reaction to perturbations (Box 1) and regularly exhibit persistent abundance fluctuations (Supporting Information II.F.2). As discussed in the following section, assessing these different metrics provides a unique fingerprint that allows us to distinguish cliques from the three other multistability regimes. The same clique fingerprint emerges under purely linear but heterogeneous interaction strengths (Supporting Information III; Bunin, 2017) or homogeneous strengths but non-uniform network connectivity ($0 < p < 1$; Supporting Information II.F.3), meaning that it does not depend on species being locally bistable. It is in this context of low network connectivity that the term *cliques* was first used to describe alternative subgroups of coexisting species (Fried et al., 2016; Supporting Information II.F).

Abundance fluctuations and stable states coexist in the clique regime. A large fraction of cliques achieves a stable fixed point when community size N is moderate as in experimental or controlled environments ($N = 10^1 \sim 10^2$; Supporting Information II.F.2; Chase, 2003; Hu et al., 2022), whereas many cliques become unstable and fluctuate in very large systems (see Discussion; Supporting Information II.F.2; Ros et al., 2022). Furthermore, the heterogeneity threshold at which cliques emerge is not sharp for $N = 50$, and different regimes and fluctuations can coexist close to this boundary (Figure 3b) (Bunin, 2017; Mallmin et al., 2023; May, 1972; Supporting Information II.F.1, III).

In the Supporting Information, we explore four other biological models, namely Lotka-Volterra communities, gene regulatory networks, cancer-immune interactions and neural networks. We find that the same four

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

multistability regimes emerge consistently across all these models, again depending on the sign and heterogeneity of the interactions at play (Supporting Information III).

Fingerprints of each multistability regime

Four different multistability regimes emerge in the species-rich community model of Equation (1). Each is driven by specific interactions and can encompass a different number of stable states (Figures 2 and 3). However, the number of states alone is not enough to characterize a given regime (Figure 3, Box 1). This raises the questions: What makes the community states in these regimes really different? and: Can our framework help us identify each regime in experimental data?

As mentioned above for cliques, key state properties are interrelated differently for each multistability regime (Figure 4). Across the studied models, global bistability scenarios have an expectedly simple signature (Figure 4a purple): they are characterized by two stable states involving all or no surviving species, a pattern that remains stable across system sizes ($\Omega(N) = 2$ and $D(N) = 0$ or N, Figure 4b; Supporting Information II.G). Moreover, the $D = N$ state is very resilient to perturbations, as cooperation between many species drastically reduces the basin of attraction of $\boldsymbol{x} = 0$ and global extinction is only observed when all species start at very low abundance (Figure 4c; Supporting Information II.B.2).

In contrast, local multistability (Figure 4a yellow) comprises many possible stable states, some of which might take very long to stabilize, resulting in apparent fluctuations (Supporting Information II.E.2). The multiplicity of states explodes when increasing species number ($\Omega(N) \sim 2^N$), a signature that would only be observable in simulations or laboratory experiments with many replicas ($N = 20$ species generate up to $\Omega \approx 10^6$ states, explaining the yellow asymptote in Figure 4b) The $\Omega(N) \sim 2^N$ trend can be observed for smaller N (Supporting Information II.G.1). An easier-to-spot fingerprint is that diversity D can take any value between 0 and N (Supporting Information II.G.2). Local states are also particularly prone to small shifts after perturbations, as any invasion or extinction follows from a species abundance crossing its Allee Effect boundary (Figure 4c; Supporting Information II.A; Box 1).

Competition drives the other two regimes at play. Under strong and homogeneous competition, states are characterized by the mutual exclusion fingerprint, involving $\Omega(N) \sim N$ states, each with a single survivor ($D(N) \sim 1$; Figure 4a,b blue). Also typical of transitive competition, these states rarely fluctuate (Soliveres & Allan, 2018).

Cliques of a few coexisting species emerge as competition becomes heterogeneous (Figure 4 green). Across the studied models we found that the number of stable cliques is larger than system size ($\Omega(N) \sim N^\theta$, $1 < \theta < 2$; Supporting Information II.F.2, II.G.1), meaning that systems with $N = 50$ can exhibit hundreds of different stable states (Figure 4b). Although there are specific settings for which the number of cliques can even be exponential in N (Altieri et al., 2021; Diederich & Opper, 1989; Supporting Information II.F), current agreement for models with uncorrelated A_{ij} values indicates that only a much smaller number of cliques is stable and uninvadable (Mallmin et al., 2023; Ros et al., 2022), in agreement with our results (Figure 4b green; Supporting Information II.F.2 and II.G.1). While the large number of cliques can be beyond experimental measurement, another key property is their constrained diversity: shifts between cliques imply some species turnover, but rarely a drastic change in species richness (Supporting Information II.G.2; Box 1). As recently observed in microbial communities (Hu et al., 2022), cliques also show a high tendency to exhibit chaotic fluctuations ($S < 1$; Figure 4a; Supporting Information II.F.2).

The resilience of states to random perturbations R correlates inversely with their multiplicity Ω, with a predictable lower resilience bound at $R \sim \Omega^{-1}$ (Figure 4c; Supporting Information II.G.3). This puts forward a relevant hypothesis in random complex systems: the fragility of states increases drastically and predictably with their number, as their agglomeration reduces their basin stability. Finally, each regime shows a distinct response to single-species extinctions, providing a useful signature in experimental settings (Box 1).

DISCUSSION

Four different multistability regimes emerge in a high-dimensional community model of interacting species under an Allee Effect. Each of these regimes emerges under a clearly identifiable interaction scheme and is characterized by a distinct measurable signature. The same regimes and signatures emerge in four other biological models. Interestingly, two of the regimes –mutual exclusion and cliques– emerge in systems that do not have species-level bistability. This shows that complex multistability can emerge without imposing specific low-dimensional constraints. In this section, we discuss (1) the links between the observed regimes and previous theoretical work, (2) the relation between their fingerprints and empirical observations in ecology and (3) the emergence of equivalent regimes across models of complex systems.

Relation with theoretical results

The results of our study contribute to a growing body of research studying multistability in species-rich communities (Bunin, 2017; Gao et al., 2016; Huisman & Weissing, 2001; Karatayev et al., 2023; Kessler & Shnerb, 2015; Lever

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

et al., 2014), where some of the regimes described above have been observed in isolation. Research on species-rich communities interacting only through cooperation identified the emergence of an all-or-nothing regime (Gao et al., 2016; Lever et al., 2014). Subsequent studies have discussed how bistability is dismantled when competitive dynamics and heterogeneity are in place (Supporting Information II.C.1; Arnoldi et al., 2016; Tu et al., 2017) as well as the role of network structure in allowing the all-or-nothing response (Karatayev et al., 2023; Lever et al., 2014; Lorenzana et al., 2023).

Another body of work has described the emergence of a complex set of multiple fixed points in species-rich communities under heterogeneous interactions without the need to impose species-level bistability (Bunin, 2017; Diederich & Opper, 1989; Supporting Information II.F, III.A). The emergence of multistability under heterogeneous interactions can be explained within the context of intransitive competition (Huisman & Weissing, 2001; May & Leonard, 1975; Soliveres & Allan, 2018): non-uniform competition strengths imply that species can beat some competitors and lose to some others, so that a single system can encode different groups of coexisting species (Gallien et al., 2017). The number and stability of these states depend on the assumptions of each ecological model (Biroli et al., 2018; Fried et al., 2016; Ros et al., 2022; Supporting Information II.F.2). Random asymmetric interactions ($A_{ij} \neq A_{ji}$) between a very large number of species ($N \to \infty$) generate mostly unstable states, associated to chaotic fluctuations in the presence of noise or species migration (Mallmin et al., 2023; Ros et al., 2022; Roy et al., 2020). This can explain the community variability or the unpredictable dynamics of some systems (Beninca et al., 2008; Hu et al., 2022; Huisman & Weissing, 2001; Mallmin et al., 2023; Supporting Information II.F.2). Alternatively, and in line with our findings, other ecological models have identified that stable cliques, i.e. small subsets of few coexisting species, can emerge if the system size is finite (Kessler & Shnerb, 2015; Mallmin et al., 2023) or the competition matrix is sparse (Bunin, 2021; Fried et al., 2016; Supporting Information II.F, III.A).

In light of previous studies, the novelty of our work is not only the description of emergent multistability, but rather how four different scenarios previously described in isolation can emerge in a single model and consistently display the same quantifiable signatures across models.

Linking the four multistability regimes to ecological evidence

The local multistability regime implies many combinations of present and absent species. Because species dynamics are weakly intertwined, environmental changes should rarely result in abrupt shifts involving many species losses, but rather gradual changes in the composition of communities (Figure 2a; Supporting Information II.G.2; Box 1). This scenario is related to the notion of ecosystems as *loose collections of species* (Gleason, 1926; Liautaud et al., 2019; Box 1), consistent with observations of gradual species replacements under environmental changes, as identified in forest (Lieberman et al., 1996; Whittaker, 1967) or benthic ecosystems (Smale, 2008). As interactions get harsher, the presence of a competitor can prevent the survival of others, reducing the multiplicity of stable states (Figure 2b) as recently observed in microbial communities (Lopes et al., 2023). A related spatial observation is that of *checkerboard* abundance distributions, where species tend to have negative associations with each other (Diamond, 1975). These patterns suggest that multiple stable states are influenced by the dominance of different competitors (Connor et al., 2013; Dallas et al., 2019).

A better-understood regime concerns the limit case of mutual exclusion under strong competition. Because they are easy to engineer via single-resource competition, multiple states with only one surviving competitor have been observed in detail in simpler systems (Aerts, 1999; Leslie et al., 1968), and more recently in species-rich communities (Amor et al., 2020; Lopes et al., 2023; Song et al., 2021).

Heterogeneous competition leads to the emergence of a regime with many small cliques of coexisting species. These states are characterized by a similar number of species (Figures 2c and 4; Supporting Information II.G), meaning that shifts between cliques imply a moderate species turnover, but no major change in diversity (Supporting Information II.G.2; Box 1). Cliques can be linked to two related empirical scenarios. First, opposed to ecosystems as loose collections of species is the notion of *communities as superorganisms* (Clements, 1936; Liautaud et al., 2019). Evidence of sharp shifts in community composition indicates that only specific subsets of species might be allowed to coexist (Hemp, 2006; Kitayama, 1992). Second, cliques can also be linked to *ecological succession* and related *priority effects*. In local multistability, the presence of one species does not alter whether a second one can invade or survive (Figure 5a). In cliques instead, historical contingencies in the order of species arrivals do affect which of many states is reached (Bunin, 2021; Drake, 1991; May, 1977; Price & Morin, 2004; Box 1, Figure 5b). Yet, it remains unclear if succession dynamics are purely unpredictable (Huisman & Weissing, 2001) or else if there exists an order explaining which cliques will be preferentially reached by community assembly (Bunin, 2021; Box 1). Clique states are also linked to the emergence of chaotic fluctuations, a signature of intransitive competition in nature (Beninca et al., 2008; Hu et al., 2022).

Finally, the global bistability regime could be linked to *catastrophic shifts*: large and abrupt transitions

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

between two markedly different states (Scheffer et al., 2001). Such a signature, however, only emerges in the studied models under very specific nonlinear and positive interactions. This is not in agreement with empirical evidence for communities undergoing catastrophic shifts in nature (Hirota et al., 2011; Scheffer et al., 1993; Schröder et al., 2005; Zaoli & Grilli, 2021), where interaction types are likely to be mixed and heterogeneous. The rarity of large transitions in the studied models is consistent with recent observations indicating that abrupt shifts are not the norm in ecosystems (Hillebrand et al., 2020), but rather emerge under specific conditions that are yet to be elucidated. Nonetheless, this leaves us with a puzzling discrepancy between models and observations, since we still don't know the general conditions by which large transitions between alternative community states can emerge. Since our study relies on random networks, we hypothesize that a missing ingredient is related to the non-random structure of real ecological networks (Bascompte et al., 2003; De Ruiter et al., 1995; Kéfi, Miele, et al., 2016; Lever et al., 2014; Rohr et al., 2014). More generally, a future research avenue is to explore how network structure affects the four regimes identified. In particular, our intuition is that, among the different regimes, the effect of non-random interactions should be especially interesting on clique states, since cliques do not require low-dimensional bistability or a dominant interaction type to emerge. Future studies should seek to understand if structured matrices can allow for species-rich and species-poor cliques, and hence large transitions between them. Testing this hypothesis would fill a fundamental gap in our understanding of catastrophic shifts in complex ecosystems.

Equivalent multistability regimes and fingerprints across complex systems

We find that the four multistability regimes described here also emerge in four other high-dimensional models: Generalized Lotka-Volterra (GLV) interactions (Bunin, 2017), the cancer-immune interplay (Garay & Lefever, 1978), gene regulatory networks (Karlebach & Shamir, 2008) and neural cluster interactions in the brain (Stern et al., 2014) (see Methods; Supporting Information III). In these models, our results highlight the same simple and generic taxonomy: Global and local states emerge in cooperative or weakly interacting systems with bistable units, while mutual exclusion states and cliques emerge in the presence of dominant competitive interactions without the need for local bistability. This explains why the GLV model does not harbour global bistability (no bistable units, $\boldsymbol{x} = 0$ is not a stable attractor) while the neural interactions model does not harbour mutual exclusion states, as extinction due to inhibition is not defined in the model (Figure 4d; Supporting Information III). Furthermore, the fingerprints of each regime are equivalent across models (Figure 4d). These results highlight a key property of high-dimensional multistability: bistability at the unit level can upscale to generate global or local multistabilities, but cliques and mutual exclusion can emerge even if the units of the system are monostable and interactions are linear (Figure 4d) (Bunin, 2017; Supporting Information II.F, III.A). This further emphasizes our need to move beyond the current low-dimensional description of alternative stable states when studying complex systems (Figure 1a).

CONCLUSION

Understanding how multiple stable states emerge in complex systems is relevant to many fields of research. In ecology in particular, it might play a pivotal role in our capacity to predict and address abrupt shifts in ecosystems (Kéfi et al., 2022). Our work highlights that the current low-dimensional understanding of alternative stable states does not easily scale up when analysing species-rich communities with multiple interaction types and random structures (Kéfi et al., 2022).

By analysing archetypical models of complex ecological communities and other biological systems, we identified the emergence of four different multistability regimes. Of these, two arise in cooperative or weakly interacting scenarios if species are locally bistable, while the other two manifests under predominantly competitive dynamics even if interactions are linear and species are not bistable. Furthermore, each regime leaves a distinct quantifiable fingerprint, providing a tool to further test their occurrence in empirical datasets.

We propose that each multistability regime can be related to well-established observations in ecology. Interestingly, across the studied models, a catastrophic shift signature only emerges under overwhelmingly positive interactions, which does not coincide with natural evidence of abrupt transitions. This allows us to hypothesize that non-random network structures are essential ingredients of community scale catastrophic shifts in ecosystems.

Our taxonomy suggests a constrained number of multistability signatures expected to generically emerge in high-dimensional biological models. These results contribute to building a unified framework to understand the nature and conditions by which multistability emerges in complex systems.

AUTHOR CONTRIBUTIONS

All authors designed the original study, GA-G performed and analysed simulations, all authors developed the mathematical analysis and discussed results, GA-G wrote the first draft of the manuscript, and all authors contributed substantially to the final version of the manuscript.

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

FUNDING INFORMATION

Fundación Ramon Areces; French National Research Agency ANR, Grant/Award Number: ANR-18-CE02-0010-01.

ACKNOWLEDGEMENTS

The authors thank the members of the BioDICée team at ISEM and the members of the Institut Natura e Teoria en Pireneus (INTP) for discussions and support throughout the project, as well as three anonymous reviewers for in-depth analysis of the original manuscript. G.A.-G. thanks L. Arola, I. Lajaaiti, B. Pichon and R. Solé for insight and feedback and A. Vives and J. Leigh for support on graphical design. Special thanks to J. G. Cole and B. Parham for inspiration. G.A.-G. was supported by a 2022 postdoctoral fellowship of the Fundación Ramón Areces. S.K. was supported by the Alexander von Humboldt Foundation and by the grant ANR-18-CE02-0010-01 of the French National Research Agency ANR (project EcoNet).

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14413.

DATA AVAILABILITY STATEMENT

Codes developed for the present article are available at https://github.com/GuimAguade/A-taxonomy-of-MSS-in-complex-ecological-communities.

ORCID

Guim Aguadé-Gorgorió https://orcid.org/0000-0001-9467-3027
Jean-François Arnoldi https://orcid.org/0000-0001-9373-4051
Matthieu Barbier https://orcid.org/0000-0002-0669-8927
Sonia Kéfi https://orcid.org/0000-0002-9678-7770

REFERENCES

Adler, P.B., Smull, D., Beard, K.H., Choi, R.T., Furniss, T., Kulmatiski, A. et al. (2018) Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters*, 21(9), 1319–1329.

Aerts, R. (1999) Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany*, 50(330), 29–37.

Altieri, A., Roy, F., Cammarota, C. & Biroli, G. (2021) Properties of equilibria and glassy phases of the random Lotka-Volterra model with demographic noise. *Physical Review Letters*, 126(25), 258301.

Amor, D.R., Ratzke, C. & Gore, J. (2020) Transient invaders can induce shifts between alternative stable states of microbial communities. *Science Advances*, 6(8), eaay8676.

Arnoldi, J.-F., Haegeman, B., Revilla, T. & Loreau, M. (2016) *bioRxiv*, 056218.

Barabás, G., Michalska-Smith, M.J. & Allesina, S. (2016) The effect of intra- and interspecific competition on coexistence in multispecies communities. *The American Naturalist*, 188(1), E1–E12.

Barbier, M., Arnoldi, J.-F., Bunin, G. & Loreau, M. (2018) Generic assembly patterns in complex ecological communities. *Proceedings of the National Academy of Sciences*, 115(9), 2156–2161.

Bascompte, J. (2007) Networks in ecology. *Basic and Applied Ecology*, 8(6), 485–490.

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003) The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100(16), 9383–9387.

Beisner, B.E., Haydon, D.T. & Cuddington, K. (2003) Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, 1(7), 376–382.

Beninca, E., Huisman, J., Heerkloss, R., Jöhnk, K.D., Branco, P., Van Nes, E.H. et al. (2008) Chaos in a long-term experiment with a plankton community. *Nature*, 451(7180), 822–825.

Biroli, G., Bunin, G. & Cammarota, C. (2018) Marginally stable equilibria in critical ecosystems. *New Journal of Physics*, 20(8), 083051.

Bunin, G. (2017) Ecological communities with Lotka-Volterra dynamics. *Physical Review E*, 95(4), 042414.

Bunin, G. (2021) Directionality and community-level selection. *Oikos*, 130(4), 489–500.

Chase, J.M. (2003) Experimental evidence for alternative stable equilibria in a benthic pond food web. *Ecology Letters*, 6(8), 733–741.

Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D. et al. (2002) The interaction between predation and competition: a review and synthesis. *Ecology Letters*, 5(2), 302–315.

Clements, F.E. (1936) Nature and structure of the climax. *Journal of Ecology*, 24(1), 252.

Connor, E.F., Collins, M.D. & Simberloff, D. (2013) The checkered history of checkerboard distributions. *Ecology*, 94(11), 2403–2414.

Courchamp, F., Berec, L. & Gascoigne, J. (2008) *Allee effects in ecology and conservation*. Oxford: OUP.

Dallas, T., Melbourne, B.A. & Hastings, A. (2019) When can competition and dispersal lead to checkerboard distributions? *Journal of Animal Ecology*, 88(2), 269–276.

De Ruiter, P.C., Neutel, A.-M. & Moore, J.C. (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science*, 269(5228), 1257–1260.

Diamond, J.M. (1975) Assembly of species communities. In: Diamond, J.M. & Cody, M.L. (Eds.) *Ecology and evolution of communities*. Boston, MA: Harvard University Press, pp. 342–344.

Diederich, S. & Opper, M. (1989) Replicators with random interactions: a solvable model. *Physical Review A*, 39(8), 4333–4336.

Dormand, J.R. & Prince, P.J. (1980) A family of embedded Runge-Kutta formulae. *Journal of Computational and Applied Mathematics*, 6(1), 19–26.

Drake, J.A. (1991) Community-assembly mechanics and the structure of an experimental species ensemble. *The American Naturalist*, 137(1), 1–26.

Fort, H. (2018) On predicting species yields in multispecies communities: quantifying the accuracy of the linear Lotka-Volterra generalized model. *Ecological Modelling*, 387, 154–162.

Fried, Y., Kessler, D.A. & Shnerb, N.M. (2016) Communities as cliques. *Scientific Reports*, 6(1), 1.

Friman, V.-P., Guzman, L.M., Reuman, D.C. & Bell, T. (2015) Bacterial adaptation to sublethal antibiotic gradients can change the ecological properties of multitrophic microbial communities. *Proceedings of the Royal Society B: Biological Sciences*, 282(1806), 20142920.

Fujita, H., Ushio, M., Suzuki, K., Abe, M.S., Yamamichi, M., Iwayama, K. et al. (2023) Alternative stable states, nonlinear behavior, and predictability of microbiome dynamics. *Microbiome*, 11(1), 1.

Gajer, P., Brotman, R.M., Bai, G., Sakamoto, J., Schütte, U.M., Zhong, X. et al. (2012) Temporal dynamics of the human vaginal microbiota. *Science Translational Medicine*, 4(132), 132ra52.

Gallien, L., Zimmermann, N.E., Levine, J.M. & Adler, P.B. (2017) The effects of intransitive competition on coexistence. *Ecology Letters*, 20(7), 791–800.

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Gao, J., Barzel, B. & Barabási, A.-L. (2016) Universal resilience patterns in complex networks. *Nature*, 530(7590), 307–312.

Garay, R.P. & Lefever, R. (1978) A kinetic approach to the immunology of cancer: stationary states properties of efffector-target cell reactions. *Journal of Theoretical Biology*, 73(3), 417–438.

Gleason, H.A. (1926) Bulletin of the Torrey botanical club. *Journal of the Torrey Botanical Society*, 102(5), 277–282.

Graham, N.A., Jennings, S., MacNeil, M.A., Mouillot, D. & Wilson, S.K. (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, 518(7537), 94–97.

Hemp, A. (2006) Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant Ecology*, 184, 27–42.

Hillebrand, H., Donohue, I., Harpole, W.S., Hodapp, D., Kucera, M., Lewandowska, A.M. et al. (2020) Thresholds for ecological responses to global change do not emerge from empirical data. *Nature Ecology & Evolution*, 4(11), 1502–1509.

Hirota, M., Holmgren, M., Van Nes, E.H. & Scheffer, M. (2011) Global resilience of tropical forest and savanna to critical transitions. *Science*, 334(6053), 232–235.

Holland, J.N., DeAngelis, D.L. & Bronstein, J.L. (2002) Population dynamics and mutualism: functional responses of benefits and costs. *The American Naturalist*, 159(3), 231–244.

Holzapfel, C. & Mahall, B.E. (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave desert. *Ecology*, 80(5), 1747–1761.

Hu, J., Amor, D.R., Barbier, M., Bunin, G. & Gore, J. (2022) Emergent phases of ecological diversity and dynamics mapped in microcosms. *Science*, 378(6615), 85–89.

Huisman, J. & Weissing, F.J. (2001) Fundamental unpredictability in multispecies competition. *The American Naturalist*, 157(5), 488–494.

Karatayev, V.A., Baskett, M.L. & van Nes, E.H. (2023) The potential for alternative stable states in food webs depends on feedback mechanism and trait diversity. *The American Naturalist*, 202(3), 260–275.

Karlebach, G. & Shamir, R. (2008) Modelling and analysis of gene regulatory networks. *Nature Reviews Molecular Cell Biology*, 9(10), 770–780.

Kéfi, S., Holmgren, M. & Scheffer, M. (2016) When can positive interactions cause alternative stable states in ecosystems? *Functional Ecology*, 30(1), 88–97.

Kéfi, S., Miele, V., Wieters, E.A., Navarrete, S.A. & Berlow, E.L. (2016) How structured is the entangled bank? The surprisingly simple organization of multiplex ecological networks leads to increased persistence and resilience. *PLoS Biology*, 14(8), e1002527.

Kéfi, S., Rietkerk, M., Alados, C., Pueyo, Y., Papanastasis, V., ElAich, A. et al. (2007) Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature*, 449, 213–217.

Kéfi, S., Saade, C., Berlow, E.L., Cabral, J.S. & Fronhofer, E.A. (2022) Scaling up our understanding of tipping points. *Philosophical Transactions of the Royal Society B*, 377(1857), 20210386.

Kessler, D.A. & Shnerb, N.M. (2015) Generalized model of Island biodiversity. *Physical Review E*, 91(4), 042705.

Kitayama, K. (1992) An altitudinal transect study of the vegetation on mount Kinabalu, Borneo. *Vegetatio*, 102, 149–171.

Koffel, T., Daufresne, T. & Klausmeier, C.A. (2021) From competition to facilitation and mutualism: a general theory of the niche. *Ecological Monographs*, 91(3), e01458.

Laska, M.S. & Wootton, J.T. (1998) Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology*, 79(2), 461–476.

Laurence, E., Doyon, N., Dubé, L.J. & Desrosiers, P. (2019) Spectral dimension reduction of complex dynamical networks. *Physical Review X*, 9(1), 011042.

Leslie, P., Park, T. & Mertz, D.B. (1968) The effect of varying the initial numbers on the outcome of competition between two *Tribolium* species. *Journal of Animal Ecology*, 37(1), 9.

Lever, J.J., van Nes, E.H., Scheffer, M. & Bascompte, J. (2014) The sudden collapse of pollinator communities. *Ecology Letters*, 17(3), 350–359.

Levin, S.A. (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. *The American Naturalist*, 104(939), 413–423.

Liautaud, K., van Nes, E.H., Barbier, M., Scheffer, M. & Loreau, M. (2019) Superorganisms or loose collections of species? A unifying theory of community patterns along environmental gradients. *Ecology Letters*, 22(8), 1243–1252.

Lieberman, D., Lieberman, M., Peralta, R. & Hartshorn, G.S. (1996) Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology*, 84, 137–152.

Litt, B., Esteller, R., Echauz, J., D'Alessandro, M., Shor, R., Henry, T. et al. (2001) Epileptic seizures may begin hours in advance of clinical onset. *Neuron*, 30(1), 51–64.

Lopes, W., Amor, D. & Gore, J. (2023) *bioRxiv*, 2023.

Lorenzana, G.G., Altieri, A. & Biroli, G. (2023) *arXiv* preprint arXiv:2309.09900.

Lozupone, C.A., Stombaugh, J.I., Gordon, J.I., Jansson, J.K. & Knight, R. (2012) Diversity, stability and resilience of the human gut microbiota. *Nature*, 489(7415), 220–230.

Mallmin, E., Traulsen, A. & De Monte, S. (2023) *arXiv* preprint arXiv:2306.11031.

May, R.M. (1972) Will a large complex system be stable? *Nature*, 238, 413–414.

May, R.M. (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, 269(5628), 471–477.

May, R.M. & Leonard, W.J. (1975) Nonlinear aspects of competition between three species. *SIAM Journal on Applied Mathematics*, 29(2), 243–253.

May, R.M., Levin, S.A. & Sugihara, G. (2008) Ecology for bankers. *Nature*, 451(7181), 893–894.

Mehner, T., Benndorf, J., Kasprzak, P. & Koschel, R. (2002) Biomanipulation of lake ecosystems: successful applications and expanding complexity in the underlying science. *Freshwater Biology*, 47(12), 2453–2465.

Menck, P.J., Heitzig, J., Marwan, N. & Kurths, J. (2013) How basin stability complements the linear-stability paradigm. *Nature Physics*, 9(2), 89–92.

Mougi, A. & Kondoh, M. (2012) Diversity of interaction types and ecological community stability. *Science*, 337(6092), 349–351.

Petraitis, P. (2013) *Multiple stable states in natural ecosystems*. Oxford: OUP.

Pilosof, S., Porter, M.A., Pascual, M. & Kéfi, S. (2017) The multilayer nature of ecological networks. *Nature Ecology & Evolution*, 1(4), 0101.

Price, J.E. & Morin, P.J. (2004) Colonization history determines alternate community states in a food web of intraguild predators. *Ecology*, 85(4), 1017–1028.

Relman, D.A. (2012) The human microbiome: ecosystem resilience and health. *Nutrition Reviews*, 70(suppl_1), S2.

Rocha, J.C., Peterson, G.D. & Biggs, R. (2015) Regime shifts in the anthropocene: drivers, risks, and resilience. *PLoS One*, 10(8), e0134639.

Rohr, R.P., Saavedra, S. & Bascompte, J. (2014) On the structural stability of mutualistic systems. *Science*, 345(6195), 1253497.

Ros, V., Roy, F., Biroli, G., Bunin, G. & Turner, A.M. (2022) *arXiv* preprint arXiv:2212.01837.

Roy, F., Barbier, M., Biroli, G. & Bunin, G. (2020) Complex interactions can create persistent fluctuations in high-diversity ecosystems. *PLoS Computational Biology*, 16(5), e1007827.

Scheffer, M. (2020) *Critical transitions in nature and society*, Vol. 16. Princeton, NJ: Princeton University Press.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, 413(6856), 591–596.

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V. et al. (2012) Anticipating critical transitions. *Science*, 338(6105), 344.

Scheffer, M., Hosper, S.H., Meijer, M.L., Moss, B. & Jeppesen, E. (1993) Alternative equilibria in shallow lakes. *Trends in Ecology & Evolution*, 8(8), 275–279.

Scheffer, M. & Jeppesen, E. (2007) Regime shifts in Shallow Lakes. *Ecosystems*, 10(1), 1–3.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. et al. (1990) Biological feedbacks in global desertification. *Science*, 247(4946), 1043–1048.

Schröder, A., Persson, L. & De Roos, A.M. (2005) Direct experimental evidence for alternative stable states: a review. *Oikos*, 110(1), 3–19.

Smale, D.A. (2008) Continuous benthic community change along a depth gradient in Antarctic shallows: evidence of patchiness but not zonation. *Polar Biology*, 31, 189–198.

Solé, R. (2011) *Phase transitions*, Vol. 3. Princeton, NJ: Princeton University Press.

Soliveres, S. & Allan, E. (2018) Everything you always wanted to know about intransitive competition but were afraid to ask.

Song, C., Uricchio, L.H., Mordecai, E.A. & Saavedra, S. (2021) Understanding the emergence of contingent and deterministic exclusion in multispecies communities. *Ecology Letters*, 24(10), 2155–2168.

Spaak, J.W., Carpentier, C. & De Laender, F. (2021) Species richness increases fitness differences, but does not affect niche differences. *Ecology Letters*, 24(12), 2611–2623.

Stern, M., Sompolinsky, H. & Abbott, L.F. (2014) Dynamics of random neural networks with bistable units. *Physical Review E*, 90(6), 062710.

Tu, C., Grilli, J., Schuessler, F. & Suweis, S. (2017) Collapse of resilience patterns in generalized Lotka-Volterra dynamics and beyond. *Physical Review E*, 95(6), 062307.

Wang, G., Liang, X.-G. & Wang, F.-Z. (1999) The competitive dynamics of populations subject to an Allee effect. *Ecological Modelling*, 124(2–3), 183–192.

Whittaker, R.H. (1967) Gradient analysis of vegetation. *Biological Reviews*, 42(2), 207–264.

Wieters, E.A. (2005) Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. *Marine Ecology Progress Series*, 301, 43–54.

Wright, D.H. (1989) A simple, stable model of mutualism incorporating handling time. *The American Naturalist*, 134(4), 664–667.

Wright, E.S., Gupta, R. & Vetsigian, K.H. (2021) Multi-stable bacterial communities exhibit extreme sensitivity to initial conditions. *FEMS Microbiology Ecology*, 97(6), fiab073.

Zaoli, S. & Grilli, J. (2021) A macroecological description of alternative stable states reproduces intra- and inter-host variability of gut microbiome. *Science Advances*, 7(43), eabj2882.

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: Aguadé-Gorgorió, G., Arnoldi, J.-F., Barbier, M. & Kéfi, S. (2024) A taxonomy of multiple stable states in complex ecological communities. *Ecology Letters*, 27, e14413. Available from: https://doi.org/10.1111/ele.14413

14610248, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14413 by SEA ORCHID (Thailand), Wiley Online Library on [14/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License