A Practical Guide to Quantifying Ecological Coexistence

Adam T. Clark[1,§*], Lauren Shoemaker[2,§], Jean-François Arnoldi[3],
György Barabás[4,5], Rachel Germain[6], Oscar Godoy[7], Lauren Hallett[8],
Canan Karakoç[9,10], Serguei Saavedra[11,12], and Sebastian Schreiber[13]

[1]Uni. Graz, Department of Biology, Holteigasse 6, 8010 Graz, Austria. ORCID: 0000-0002-8843-3278.
[2]Botany Department, University of Wyoming, Laramie, USA 82071
[3]Centre National de la Recherche Scientifique, Experimental and Theoretical Ecology Station, Moulis, France.
[4]Division of Biology, Linköping University, SE-58183 Linköping, Sweden. ORCID: 0000-0002-7355-3664.
[5]Institute of Evolution, Centre for Ecological Research, Konkoly-Thege Miklós út 29-33, H-1121 Budapest, Hungary.
[6]Dept. of Zoology, The University of British Columbia, Vancouver, BC, CA, V6T1Z4.
[7]Estación Biológica de Doñana (EBD-CSIC) Americo Vespucio 26, 41092, Sevilla, Spain. ORCID: 0000-0003-4988-6626.
[8]Institute of Ecology and Evolution, University of Oregon, Eugene, Oregon, USA. ORCID: 0000-0002-0718-0257
[9]School of Biological Sciences and Center for Microbial Dynamics and Infection, Georgia Institute of Technology, Atlanta, GA 30332, USA. ORCID: 0000-0002-3921-3535
[10]Department of Biology, Indiana University, Bloomington, IN 47405 USA.
[11]Department of Civil and Environmental Engineering, MIT, 77 Massachusetts Avenue, Cambridge, MA 02139, USA. ORCID: 0000-0003-1768-363X
[12]Santa Fe Institute, 1399 Hyde Park Rd, Santa Fe, NM 87501, USA
[13]Department of Evolution and Ecology and Center for Population Biology, University of California, Davis, USA 95616
[*]Corresponding author contact: adam.clark@uni-graz.at
[§]Both authors contributed equally to the manuscript.

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Abstract

Coexistence is simultaneously one of the most fundamental concepts of ecology, and one of the most difficult to define and quantify. A particular challenge is that, despite a well-developed body of research on the subject, several different schools of thought have developed over the past century, leading to multiple independent, and largely isolated, branches of literature with distinct methodologies. Here, we provide a broad overview of the most common concepts and metrics currently used to detect and quantify ecological coexistence. We first introduce four classes of behaviour that describe different aspects of community dynamics: (i) the existence of a feasible steady state, i.e. where all coexisting species retain positive abundances in the long-term in the absence of interference by external forces; (ii) the existence of a local attractor that draws the community towards a feasible steady state from within a restricted set of starting conditions; (iii): the existence of a global attractor that draws the community towards feasible steady states from any non-zero starting condition; and (o) a null transient state, where species abundances vary over time irrespective of steady states and attractors. Next, we explain how these classes of behaviour relate to commonly used metrics for classifying and quantifying coexistence, including analyses of parameter sensitivity, asymptotic return rates, invasion growth rates, and time to extinction. We then discuss the scope and limitations of each of these behavioural classes and corresponding metrics, with a particular focus on applications in empirical systems. Finally, we provide a potential workflow for matching empirical questions to theoretical tools, and present a brief prospectus looking forward to opportunities to better advance and integrate research on quantifying coexistence.

Key words: ecological coexistence, parameter sensitivity, structural stability, asymptotic return rate, invasion growth rate, mutual invasibility, time to extinction, empirically tractable

Contents

1 Introduction

Understanding how and when species coexist is one of the primary goals of ecology (MacArthur 1972). Accurate predictions of the circumstances under which communities of species are likely to coexist is also a fundamental prerequisite for addressing many of the discipline's most pressing challenges, with potential applications including effective design of conservation and restoration strategies (Bradshaw 1992), identifying and managing invasive species (Moles et al. 2008), estimating rates of biodiversity change and turnover (Newbold et al. 2015, Blowes et al. 2024), and forecasting impacts of global change (Sage 2020, Usinowicz and Levine 2018, Van Dyke et al. 2022). However, despite almost a century of theoretical advances in our understanding of coexistence, the field remains largely fractured, resulting in multiple schools of thought with their own distinct definitions for what qualifies as coexistence, and surprisingly few attempts to reconcile these dominant frameworks and their corresponding metrics (Lawton 1999, Donohue et al. 2016).

Within the coexistence literature, it has been especially challenging to synthesise insights about coexistence across empirical studies. This challenge arises due to both the literature's fragmentation in the definitions and metrics used to quantify coexistence, and because existing metrics are often challenging to apply in real world contexts, requiring both empirical and analytical expertise, ample data, and strong theoretical assumptions (Levine et al. 2017, Clark et al. 2019, Spaak et al. 2023). Arguably as a consequence, there are currently no cross-system meta-analyses or "global studies" of coexistence, and surprisingly, little is known about how opportunities for coexistence compare across space, time, and species.

This review seeks to provide a high-level overview of recent advances in coexistence theory, with the goal of summarising disparate literatures for theoreticians and empiricists alike, both for ecologists new to coexistence, or those who are experts in a given set of classes and metrics for determining coexistence. We aim for the review to highlight strengths and weaknesses between the different threads of the coexistence literature, with an eye towards practical applications in real world systems. We begin with a brief summary of the historical development of coexistence theory and explain how it shaped the modern concept of coexistence (Section 2). Next, we introduce the most common kinds of dynamical behaviour currently used by theorists to describe coexistence (Section 3.1), and, correspondingly, the most common metrics used to identify these behaviours (Section 3.2). We then provide a more detailed discussion of the general challenges that empirical systems pose for efforts to characterise and measure coexistence (Section 4.1). Finally, we present guidelines and a recommended workflow for matching empirical questions to theoretical tools (Section 4.2), and suggest potential ways forward for the practical study of coexistence (Section 4.3).

1.1 Glossary

- **Coexistence:** For the purposes of this review, we broadly use “coexistence” to describe the ability of a community of co-occurring species to persist across a defined set of spatial and temporal scales. Most other published sources provide more specific definitions explained below, e.g. related to *steady states* or *stability* – however, these definitions also vary widely across sub-fields and sources. To avoid ambiguity, we therefore refer to the specific kinds of dynamical behaviour described in section 3.1 when more precise definitions of coexistence are necessary.

- **System state:** A measurement of the dynamical variables in a system at a given moment in time. In ecology, states usually refer to the abundance or biomass of organisms within a community.

- **Parameters:** Variables that govern the dynamics of states according to an equation, such as a population model – e.g. intrinsic growth rates, carrying capacities, or species interaction coefficients. Unlike states, parameters are constant for a given set of environmental conditions.

- **Steady State:** A system state or set of states which the system remains within through time in the absence of interference by external forces. Ecological studies often focus on the concept of *equilibria* – e.g. a set of species abundances that remain fixed at a set of single values over time. More generally, *invariant sets* include a wider range of dynamical behavior, describing a set of states that a system will remain within in the absence of external interference. Invariant sets include periodic and quasi-periodic orbits and chaotic motions. This broader definition is especially important for community dynamics such as predator-prey oscillations or bounded chaos. For simplicity, unless specified otherwise, we will use the term “steady state” to refer both to classic equilibria, and to invariant sets more broadly.

- **Feasibility:** In ecology, feasibility describes a state in which all species in a community have positive abundances (i.e. greater than zero; a self-evident empirical requirement that is sometimes overlooked in models). Note, however, that a feasible state does not necessarily imply a steady state, nor is it necessarily *stable*, e.g. it need not be associated with an *attractor*.

- **Attractor:** A steady state to which a system can return following externally driven changes to the state variables (e.g. as observed with the "classic" concept of a stable equilibrium). For a *local attractor*, systems only return to steady state if perturbations are sufficiently small (determined by the size and properties of the attractor), whereas for a *global attractor*, all feasible starting states lead to the same steady state. *Permanence* describes systems with global attractors where the corresponding steady state is also feasible.

- **Necessary and Sufficient Conditions:** For any theoretical outcome, necessary conditions must be met for the outcome to take place, but they do not guarantee that it will. In contrast, a sufficient condition guarantees that an outcome will take place, but does not necessarily need to be met in order for the outcome to occur. For example, the existence of a feasible equilibrium is necessary (but not sufficient) for permanence, whereas permanence is sufficient (but not necessary) for the existence of a feasible equilibrium (Hofbauer and Sigmund 1998).

2 History of Theoretical Development

Coexistence has been a central tenet of population and community ecological theory since the discipline's earliest beginnings. Efforts to model community dynamics published in rapid succession by Lotka (1925) and Volterra (1926) both discuss coexistence criteria, with Volterra in particular providing a detailed theoretical derivation of the necessary conditions for various forms of stable coexistence across different community structures (see definitions in Section 1.1).

These early theoretical and empirical findings were immensely influential for subsequent studies of coexistence. In particular, Gause's empirical tests of Lotka's and Volterra's coexistence theories popularised the competitive exclusion principle, which hypothesised that in order to coexist, species needed to differ in terms of their biological needs or ecological niches (Gause 1934). This hypothesis inspired a proliferation of empirical studies that sought to identify the biological factors that enabled coexistence for particular groups of species (e.g. MacArthur 1958, Park 1962, Paine 1966). The hypothesis was formalised mathematically by Nicholson (1933), with a later generalization by Levin (1970) who showed that for a large class of models, the number of stably coexisting species could not exceed the number of limiting factors (called "control factors" in Nicholson 1933). These limiting factors are often interpreted as specific resources such as light or nitrogen (e.g. R^* theory, Tilman 1982), though Levin was careful to note that they could also represent any combination of variables that had independent effects on species' per-capita growth rates.

Levin's and Nicholson's work showed that limiting factors were critical for understanding the conditions under which coexistence was possible – but also that identifying these factors in practice was likely to be "extremely difficult" for at least two reasons (Levin 1970, p. 416). First, although biological systems include many different interacting species and environmental variables, these variables also tend to be highly correlated in observational data – thereby complicating efforts to identify the number of independent dimensions acting on growth rates (Ellner 1988). Second, because species often exhibit non-linear growth responses to factors such as resource availability or the abundance of competitors, spatial or temporal variability can cause individual variables to "act" like multiple independent factors, e.g. with periods of low vs. high resource availability differentially affecting different species' growth functions (Levins 1979, Armstrong and McGehee 1980), or changes in the relative availability of limiting resources leading to spatio-temporal variability in species abundances and dominance structures (Tilman 1982).

To overcome these challenges, two main paradigms emerged for studying coexistence while circumventing the need to explicitly identify limiting factors: analyses of *asymptotic return rates* and of *invasion growth rates* (Turelli 1978) (see Section 3.2 for details). Asymptotic return rates describe the tendency of systems to return to steady state following small perturbations, and have their origins in applied mathematics and physics. Their use became popular in ecology following applications by MacArthur and his contemporaries for analysing competitive interactions (MacArthur 1958, 1970, 1972). The metric proved particularly effective for assessing coexistence in systems with many interacting species or resources (May and MacArthur 1972, May

1973) – especially in cases where coexistence emerged as a direct result of these interactions (Holt 1977, Lawlor 1979). An important finding of these studies was that asymptotic recovery in ecological communities is largely governed by the degree to which species interaction coefficients are linearly independent (MacArthur 1970, Chesson 1990a), thus suggesting that empirically measuring interaction strengths might be an effective way to predict and classify coexistence in real world settings (May and MacArthur 1972).

Analysis of invasion growth rates yielded a practical metric for identifying coexistence that could be estimated analytically, from model simulations, or even in invasion experiments (MacArthur and Levins 1967, Turelli 1978, Chesson and Warner 1981), with the general intuition that, if each species in a community could increase from rarity with other species at equilibrium, then species should generally coexist (though see Pande et al. 2020). Initially, studies stressed that its validity as a test for stable coexistence had "not yet been proven" (Turelli 1981, 1986). Indeed, an uncritical reliance on invasion growth rates has turned out to be mathematically naive (Barabás et al. 2018), though careful and mathematically rigorous justifications would eventually be provided through the development of permanence theory (Hofbauer 1981, Butler and Waltman 1986, Schreiber 2000). These analyses quickly gained in popularity, both because they often yielded simpler, more mathematically tractable predictions than analyses of asymptotic return rates, and because they were better able to account for effects of large disturbances and complex community dynamics, rather than just small perturbations around a static equilibrium (Turelli 1980, 1981).

In particular, a ground-breaking series of articles by Peter Chesson leveraged invasion analyses to catalog the ways in which coexistence can arise as a result of environmental fluctuations across time (Chesson 1994) and space (Chesson 2000b). Chesson's theories would eventually become the dominant framework used for explaining why species are able to coexist in spatially or temporally variable environments (see Section 3.3 for more details) – to the point that later authors came to refer to his work as "Modern Coexistence Theory" (Mayfield and Levine 2010, HilleRisLambers et al. 2012, Grainger et al. 2019), in an apparent nod to the Modern Evolutionary Synthesis.

3 Current Paradigms and Metrics

Although "classic" approaches for assessing coexistence are still commonly used by ecologists today, many of these methods have been refined to better account for important aspects of real world ecological systems (see discussion in 4.1, below). This methodological diversity has added important tractability and nuance to coexistence theory, but it also poses a problem: different methods define coexistence in distinct, and sometimes even contradictory ways – and, indeed, often make conflicting predictions (Turelli 1978).

To compare and contrast this sea of methods, we first introduce four broad classes of dynamical behaviour that ecologists tend to focus on when studying coexistence (Section 3.1). These behaviours roughly correspond to the different definitions of coexistence (or lack thereof) that are applied in contemporary theoretical studies. We then discuss metrics that are commonly used to identify and quantify each of these four behavioural regimes (Section 3.2), as well as their scope and limitations. Challenges associated with applying these metrics in empirical systems are discussed in more detail in the following section (Section 4).

3.1 Classes of Dynamic Behaviour

Species dynamics can be broadly grouped into four main classes of behaviours (Fig. 1). These behaviours are: *(i)* **feasible steady states** – systems that can remain at steady state where all species have positive abundances (3.1.1); *(ii)* **feasible local attractors** – systems with local attractors that draw species towards feasible steady states given a specific set of positive starting abundances (3.1.2); *(iii)* **feasible global attractors** – systems with a global attractor that draws species towards some set of feasible steady states (potentially including multiple different local attractors) from any starting condition with a set of non-zero species abundances (3.1.3); and, finally, *(o)* **transient states** – a state in which species abundances vary over time either without or prior to settling into a steady state that may or may not yield coexistence (3.1.4).

Each of these behaviours relates to somewhat different aspects of coexistence and stability. In practical terms for real world communities: *(i)* a feasible steady state implies that species will persist together in the long-term so long as they remain undisturbed by external forces; *(ii)* a local attractor implies that species can recover back to a steady state following small disturbances of the population abundances; *(iii)* a global attractor implies that the community can recover even from large disturbances; and *(o)* transient dynamics imply that the system is in transition, and species will either eventually go extinct or the system's dynamical behaviour will switch to one of the three other regimes. In the absence of demographic stochasticity (see Section 4.1.3), behaviours *i-iii* also follow something of a nested hierarchy: a feasible steady state is a necessary (but not sufficient) condition for a feasible local attractor, which is itself a necessary (but again, not sufficient) condition for a feasible global attractor. We compare these dynamics to transient systems, as transient dynamics can maintain co-occurrence on ecologically relevant timescales, even if long-term coexistence and stability are not expected. Below, we introduce these behaviours in more detail.

3.1.1 Feasible Steady State

A feasible steady state describes conditions for which coexisting species' abundances remain at fixed positive values over time (when at an equilibrium) or constrained within a given set of positive values (for invariant sets more generally, e.g. limit cycles). An intuitive example is carrying capacity in the logistic growth model – if a single species begins at its carrying capacity, then it will remain there in the absence of interference by external forces. Feasible steady states are necessary for long-term coexistence (although they do not guarantee it). Thus, the breakdown of a feasible steady state implies either extinction of some species, or that the system will become transient as it moves towards some other dynamical regime. In theoretical models, testing for feasible steady states is usually the first step before subsequent analyses of *stable* coexistence can proceed (Dormann 2008). This step is important not only because negative abundances are logically impossible, but also because they can produce nonsensical effects in models – e.g. in the gen-

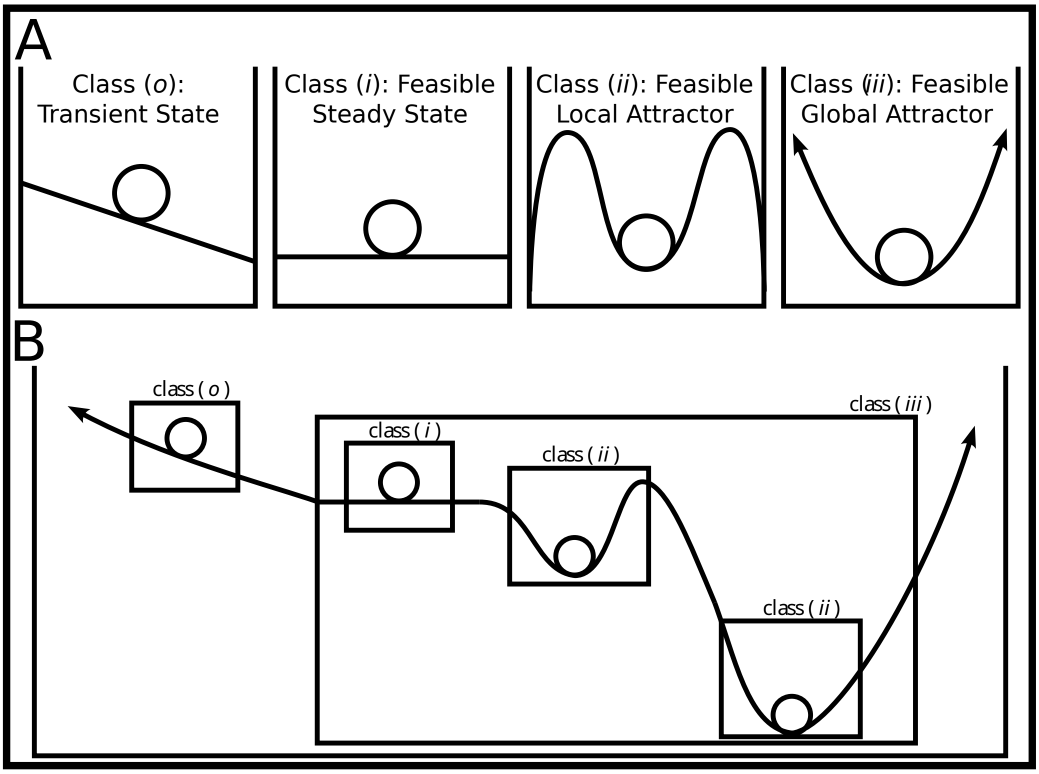


Figure 1: Four main classes of behaviour describing species abundance dynamics in the context of coexistence. **(a)** Conceptual illustration of abundance dynamics following each of the four behaviour classes discussed in Section 3.1, using a ball-and-cup metaphor. The position of the ball represents the system state (e.g. the abundance of a particular species), and the rolling trajectories in panels *o*-*iii* represent a lack of steady state, the presence of a feasible steady state, a feasible local attractor, and a feasible global attractor, respectively. Arrows around the global attractor in class *iii* indicate that the landscape extends infinitely in both directions. **(b)** An example dynamic landscape combining all four of the classes of behaviour as part of a single system. Note that dynamical behaviours within subsections of the system can follow different combinations of behaviours *o*-*ii*. The feasible steady states in class *i* plus the two feasible local attractors in class *ii* jointly make up the system's global attractor (class *iii*). In this example, in the long-term, the system is drawn away from transience and towards at least one of these states from any feasible starting state, with the precise end-state dependent on initial conditions.

eralised Lotka-Volterra equations, a competitor with negative abundance has the same effect on other species' per-capita growth rates as a mutualist with positive abundance.

Especially in models that include many different potential steady states (such as alternate stable states; see the two boxes labelled "class (*ii*)" in Fig. 1B), testing for feasibility can be laborious, as it requires first recognising and discarding all infeasible steady states that include negative abundances (Anderson et al. 1992, AlAdwani and Saavedra 2020, 2022). Nevertheless, identifying feasibility criteria can sometimes be more analytically tractable than other coexistence metrics (e.g. testing for the existence of an attractor), which has led to the use of feasibility as an independent proxy for the possibility of coexistence in some studies (Saavedra et al. 2017, Grilli et al. 2017, Song et al. 2018, see Section 3.2.1 for more details). Although most of these studies of feasible coexistence have focused on equilibria, these approaches sometimes can be applied to more complex invariant sets – e.g. to identify ranges of model parameters that lead to oscillatory cycles or even chaos (Barabás et al. 2012, Barabás and Ostling 2013, Bunin 2017, McCann and Yodzis 1994).

3.1.2 Feasible Local Attractor

Local attractors ensure that some range of starting conditions exist from which the system will be drawn towards a steady state. This range of starting conditions is called the "basin of attraction" of the attractor, and is often visualised as valleys in classical ball-and-cup diagrams such as Figure 1. Feasible local attractors support coexistence by counteracting interference by external forces, such as small environmental perturbations, that might otherwise drive species away from a feasible steady state, and towards extinction. Indeed, in the absence of an attractor, a sequence of arbitrarily small perturbations will, in the long-term, drive species to extinction (Schreiber 2006). Local attractors, however, only predict dynamics in the range of starting conditions from which the system tends towards the attractor. Thus, the existence of a feasible local attractor does not necessarily guarantee long-term coexistence – e.g. if initial abundances fall outside of the range of influence of that attractor (i.e. outside of the surrounding "valley" in the ball-and-cup diagram), or species are subjected to sufficiently strong perturbations, then long-term abundance dynamics can be driven away from the initial steady state, and towards other system states, such as those associated with alternate community structures or even species extinction (Almaraz et al. 2024).

Although the tractability and accuracy of different approaches for studying local attractors can vary, they all essentially share the same goal: to characterise dynamics around steady states based on their asymptotic return rates, and extrapolate whether dynamics are likely to remain in that state or to move towards another dynamical regime (Turelli 1978). Early work by Lewontin (1969), Levin (1970), MacArthur (1970), and May (1973), for example, identified local attractors by computing the eigenvalues for the Jacobian matrix near model equilibria. These approaches are still popular today, and are discussed in more detail in Section 3.2.2. For more general classes of invariant sets (e.g. oscillatory dynamics, chaos), local attractors can be identified by calculating return rates along the entirety of the system's dynamical trajectory, e.g. via bifurcation analysis or using Lyapunov exponents. These approaches are discussed in Section 3.2.2.1.

3.1.3 Feasible Global Attractor

In ecology, feasible global attractors refer to system dynamics in which a set of species are drawn towards feasible steady states from any feasible starting abundance – thereby meeting the criteria for *permanence*. Feasible global attractors therefore ensure long-term coexistence even in the face of strong disturbances and major re-mixing of a community. So long as perturbations do not push a species to an abundance of zero, they will always be able to recover in the long-run. This strong form of coexistence comes at the cost of more strict requirements for feasible global attractors to even exist. Indeed, their existence necessarily excludes several classes of behaviours that might be considered "coexistence" under other definitions. For example, systems subject to Allee effects – where species must exceed some minimum abundance to achieve positive growth (Fukami and Nakajima 2011, Jang 2013) – preclude feasible global attractors, as do systems where co-occurrence is transient, even if it is long-lasting.

The especially broad scope of global attractors also comes with technical challenges. Identifying and testing for them can be difficult, but invasion analysis was introduced as a more tractable approach for identifying these global attractors (Turelli 1978, Hofbauer 1981, Schreiber 2000). The general idea behind invasion analysis is that if all species in a community can increase in abundance when rare, then the system should be able to recover from most kinds of major disturbances – and that this behaviour is, at the very least, consistent with the existence of a feasible global attractor (e.g. Turelli

1981, 1986, though see Barabás et al. 2018 for theoretical limitations and Schreiber 2000, Hofbauer and Schreiber 2022 for some counterexamples). The development of permanence theory in the early 1980's provided more rigorous mathematical justification for these approaches, summarising the circumstances under which invasion analyses are sufficient for proving the existence of a global attractor (Hofbauer 1981, Butler and Waltman 1986, Garay 1989, Schreiber 2000). Analyses of invasion growth rates remain in wide use today and are discussed in more detail in Section 3.2.3.

3.1.4 Transient State

In ecology, transient states refer to abundance dynamics varying either before, or without, reaching a steady state (Hastings 2004, Fukami and Nakajima 2011). Transient dynamics can be short or long-lasting, and may or may not ultimately drive communities towards feasible steady states in the long run – although in the absence of feasible steady states, the long-term fate of any species is extinction (Murdoch 1994). In practice, it can be challenging to determine whether a particular dynamical trajectory is truly transient, is in a basin of attraction, or is even part of some more complex invariant set such as a limit cycle. Due to this ambiguity, categorising something as a transient state usually implies that no steady states that influence the current state have *yet* been identified, but often does not definitively exclude the possibility of their existence.

3.2 Metrics for Characterising Behaviours

Most contemporary studies rely on metrics that quantify specific aspects of coexistence, rather than focusing on general classes of dynamical behaviours themselves. The most widely used of these include: (*i*) **parameter sensitivity** – the quantification of how slight changes in parameter values alter system attributes, such as the existence and identity of species in feasible steady states (3.2.1); (*ii*) **asymptotic return rate** – the rate at which systems are drawn towards or away from a particular steady state (3.2.2); (*iii*) **invasion growth rate** – the rate at which species are able to increase from low abundance (3.2.3); and (*o*) **time to extinction** – the average length of time for which species maintain positive population sizes (3.2.4). Importantly, each of these metrics relates to one or more of the dynamical behaviours discussed in Section 3.1: parameter sensitivity is useful for assessing the robustness of steady states to uncertainty in, or perturbations to, parameter values; asymptotic return rates can be used to identify local attractors; invasion growth rates can be applied to test for the existence of a feasible global attractor; and time to extinction can be calculated for any kind of abundance dynamic, including transient states that yield co-occurrence on ecologically relevant timescales (Fig. 2). Below, we introduce these metrics in more detail, with a particular focus on how they are applied in practice.

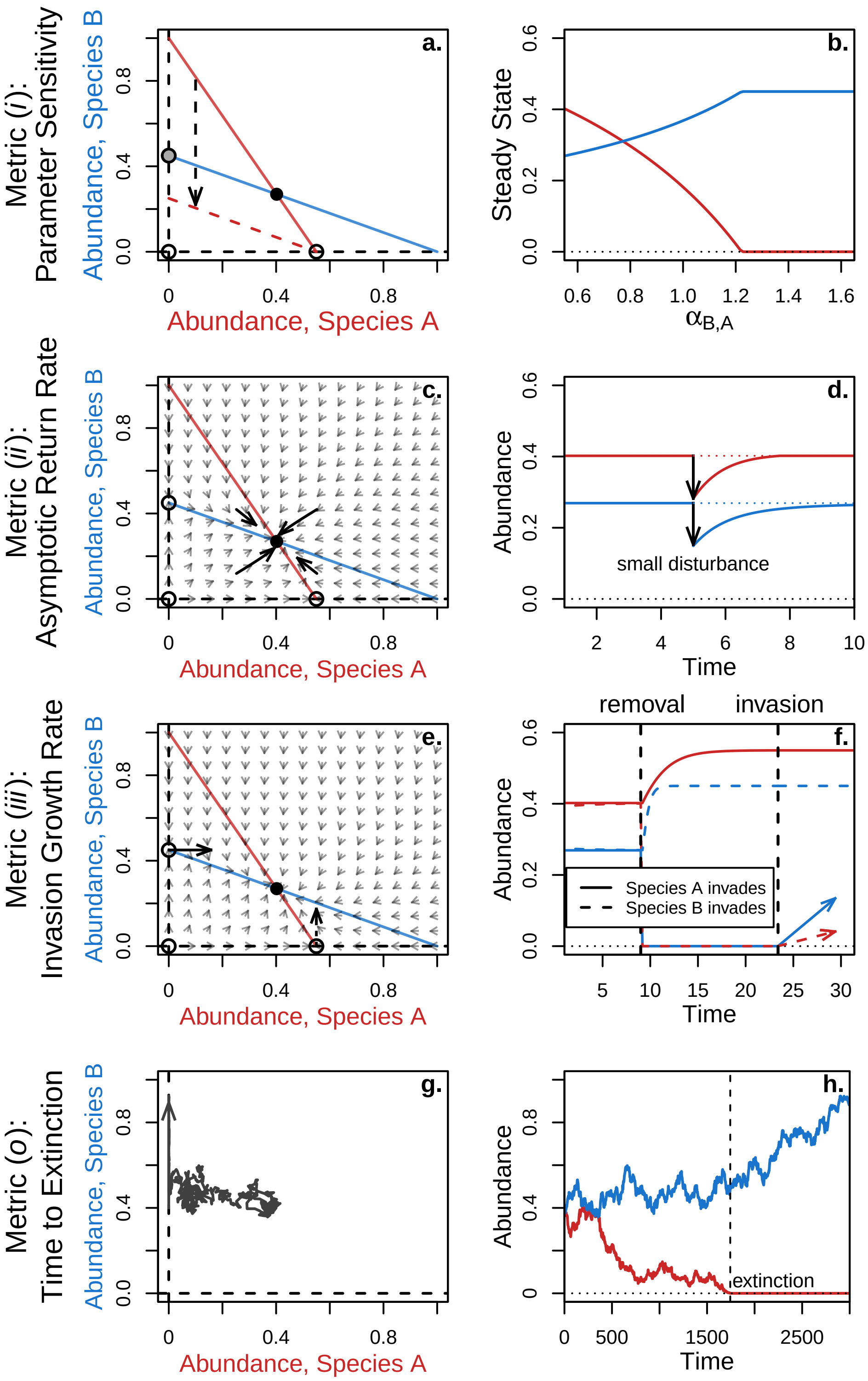


Figure 2: Caption on next page.

Figure 2: Conceptual illustration of the coexistence metrics in Section 3.2. Left column shows phase diagrams. Red and blue lines, respectively, show abundances at which species A and B experience zero net growth ("zero net growth isoclines"); empty circles show unstable equilibria; and filled circles show feasible attractors. Black arrows emphasise the main dynamics of interest for each metric. Right column shows corresponding time-series (b, f, h) or impacts of parameter changes (d), for each species. Time to extinction (*o*) is shown for a random walk with two species (thick black line and arrow). Remaining panels show results for the two-species Lokta-Volterra competition equations. Parameter sensitivity (*i*) is demonstrated via changes in $\alpha_{B,A}$, which describes the impact of species B on the per-capita growth rate of species A. The black dashed arrow shows the shift in the isocline associated with the parameter change, shifting the solid red isocline to the dashed red and causing a previously unstable equilibria to become stable (light grey circle). Asymptotic return rates (*ii*) are demonstrated in response to a series of small perturbations around the feasible equilibrium – small grey arrows show the gradient of the system's dynamics, and the thick black arrows show return trajectories. Invasion growth rates (*iii*) are shown with solid and dashed arrows at the time of invasion, representing growth trajectories starting from low abundance for species A and B, respectively, with the competitor species at its single-species carrying capacity.

3.2.1 Parameter Sensitivity

Parameter sensitivity is related to the general mathematical concept of "structural stability," which focuses on whether the topological features of a dynamical system are preserved under small perturbations of its underlying equations or parameter values (Smale 1967, Levin 1970). Structural stability can be applied in studies of coexistence to examine the conditions under which global attractors break down into local attractors, or to identify critical points where small changes in parameters alter the system's stability, such as switching from an equilibrium to a periodic solution (Almaraz et al. 2024). In a growing body of ecological studies, however, the concept of structural stability has been defined somewhat more narrowly, to test whether small perturbations to model parameters lead to the breakdown of feasible steady states (Rohr et al. 2014).

Having grown out of this focus on steady states, analyses of parameter sensitivity in ecology typically take one of two approaches. The first focuses on the range of model parameter values within which feasible steady states can be maintained for a particular subset of species (May 1973, Svirezhev and Logofet 1983, Grilli et al. 2017, Saavedra et al. 2017, 2020, Deng et al. 2022, Allen-Perkins et al. 2023). This approach provides a general overview of which regions of parameter space allow for coexistence and which regions do not. For example, under the Lotka-Volterra competition equations, if species A and B initially coexist, then increasing the competitive impact of species B on species A will eventually drive species A extinct (Fig. 2a, b). The second approach examines localised effects of perturbations. It takes a known steady state, and examines the sensitivity of that steady state to small parameter perturbations (Vandermeer 1970, Levins 1974, Meszéna et al. 2006, Barabás et al. 2014). Steady states that are oversensitive to even very small changes in the parameters (e.g. with a shallow basin of attraction) are not expected to exist for long, and are thus assumed to not allow for coexistence in the long-term. While this second method forgoes giving a global description of coexistence in parameter space, it has key advantages. Most importantly, since it relies on perturbation calculus near a known feasible steady state, it can, in principle, be applied to arbitrarily complicated dynamics (whereas global descriptions are more difficult to generalise across scenarios).

If the range of parameters allowing feasible steady states is large, those steady states are said to be “robust” against parameter perturbations. In biological terms, species will have more opportunities to coexist by withstanding a larger range of external environmental changes that impact their parameter values (e.g. growth rates, carrying capacities). This perspective has been especially effective at elucidating how different processes contribute to coexistence – e.g., disentangling how multiple limiting factors contribute to coexistence and rigorously connecting these insights back to species’ ecological roles in a way that is independent of model details (Meszéna et al. 2006, Barabás et al. 2014, Pásztor et al. 2016), quantifying the relative effects of pairwise vs. indirect interactions on equilibria in the Lotka-Volterra competition equations (Saavedra et al. 2017, García-Callejas et al. 2021), predicting which species have larger persistence times (Allen-Perkins et al. 2023, Domínguez-Garcia et al. 2024), or dividing feasibility criteria into stabilising and equalising components (Godoy et al. 2018), analogous to classic partitions of invasion growth rates as discussed in Section 3.3.

For equilibria, parameter sensitivity can be computed relatively easily – either by identifying combinations of parameter values that lead to zero net population growth for all species in the community, or by simulating the model forward in time until it reaches a feasible equilibrium. However, parameter sensitivity can also be computed for more complex dynamics (Barabás et al. 2012, Barabás and Ostling 2013, Barabás et al. 2014), or even based on empirically observed time-series data. For example, several recent studies have extended the scope of parameter sensitivity analyses to include effects of large perturbations (Tabi et al. 2020, Medeiros et al. 2021), spatially and temporally structured environments (Saavedra et al. 2020, García-Callejas et al. 2021, Luo et al. 2022, Song et al. 2023, Long et al. 2024), and nonlinear conditions for specifying steady states (Cenci and Saavedra 2018a).

3.2.2 Asymptotic Return Rate

Asymptotic return rates describe the long-term response of a dynamical system to infinitesimally small perturbations by external forces. In ecological studies of coexistence, asymptotic return rates are usually applied to track the ability of species abundances to return to a particular steady state. If these return rates indicate that the system will always be drawn back towards that steady state regardless of the direction of the perturbation, the system is said to be *asymptotically stable* (Fig. 2c, d). Tests of asymptotic stability are analogous to testing for the existence of a local attractor – i.e. proving asymptotic stability is sufficient for identifying a local attractor. Thus, asymptotic stability around a feasible steady state implies coexistence, provided that species initial abundances fall within the region of the local attractor and that interference by external forces is sufficiently small that it does not push species out of this region.

For equilibria, asymptotic stability is tested by quantifying the return rates from small perturbations around the equilibrium by computing the eigenvalues of the Jacobian matrix. The details of this procedure are beyond the scope of this review (see Otto and Day 2011 for an excellent introduction), but in essence, eigenvalues summarise rates of change along a set of transformed axes (analogous to principal component axes), which make it easier to quantify net effects of different combinations of perturbations and species dynamics. If the eigenvalues indicate that all species are drawn back towards equilibrium following small perturbations, then the system is asymptotically stable. Different indicator criteria must be used depending on the kind of system. For continuous-time systems in which population dynamics play out smoothly over time, e.g. as might be expected for algae or bacteria, the return towards equilibrium occurs if the real part of the leading eigenvalue is negative (i.e. the eigenvalue with the largest non-imaginary component). For discrete-time systems in which population dynamics occur at regular intervals, e.g. as might be assumed for annual plants or some insects, the absolute value of the largest eigenvalue in magnitude (the "dominant" eigenvalue) must be less than one. Several studies have also proposed methods for unifying the concepts of structural stability (described above) and asymptotic stability as part of a single analysis (Arnoldi and Haegeman 2016, Song and Saavedra 2018, Medeiros et al. 2021) – although these approaches are not yet in wide use.

There are several important considerations for interpreting asymptotic return rates. First, eigenvalues alone do not indicate whether a corresponding equilibrium is feasible; as such, equilibria that include non-positive species abundances must be discarded prior to analysis (Dormann 2008, Saavedra et al. 2017). Moreover, assessing only a subset of eigenvalues, or focusing only on their sign but not their magnitude, can give a misleading picture of community dynamics as a whole. This is because species within a community can present different recovery dynamics. For example, the leading eigenvalue – which is often reported as a stand-alone index of asymptotic stability – is primarily determined by the long-term recovery rate for the slowest dynamical component of the system. Thus, even if only a single rare species fails to recover from a perturbation, the real part of the corresponding leading eigenvalue will still indicate a lack of asymptotic stability for the entire community (Arnoldi et al. 2016, 2018). Similarly, this property can be misleading in systems that are subject to repeated perturbations, as the leading eigenvalue typically only includes information on long-term responses, rather than short-term dynamics (Arnoldi et al. 2018).

3.2.2.1 Dynamic approaches for assessing return rates Real world communities tend to be highly dynamic, which limits the utility of methods that focus on systems near equilibrium (Pimm et al. 2019). Although theoretical methods exist for analysing asymptotic stability in systems with more complex dynamics – e.g. that converge towards invariant sets such as limit cycles or quasi-periodic orbits (Sell 1966, Hirsch et al. 1970, Breunung 2022) – applying these metrics in practice can be difficult. The problem is two-fold. First, given an observed dynamical trajectory, it no longer suffices to test asymptotic return rates around a single fixed point – rather, return rates must be calculated along the entirety of that trajectory. Second, even if the observed part of a trajectory can be shown to be an attractor such that nearby states will always converge to it, there is no guarantee that the trajectory corresponds to long-term coexistence. For example, given any feasible starting abundance, dynamical trajectories for a logistic growth model with $r < 0$ will converge, but that convergence will be towards extinction rather than coexistence.

To address these challenges, an increasingly common approach is to apply forecasting tools such as *empirical dynamic modelling* (EDM) to approximate community dynamics, and then analyse the stability of the resulting model (Sugihara 1994, Deyle et al. 2016). EDM uses time-series observations to fit a series of piecewise locally weighted linear regressions that jointly describe how abundance dynamics, interactions among species, and environmental covariates change over time. Estimates of the Jacobian matrix describing community dynamics at each time step can then be computed directly from these piece-wise regressions. Asymptotic stability is then tested in one of two ways: either individual estimates of the Jacobian matrix are used to identify a potential equilibrium towards which the system is drawn (Ushio et al. 2018), or the full set of Jacobian Matrices can be applied to approximate their corresponding "Lyapunov spectrum" (effectively a time-varying generalisation of eigenvalues, which describe return rates along a dynamic trajectory) (Oseledec 1968). In addition to assessing asymptotic return rates, these time-varing estimates of the Jacobian matrix can also be used to assess parameter sensitivity, as discussed in 3.2.1 (Cenci and Saavedra 2019). For a more detailed review of EDM, including a discussion of available software for carrying out analyses, see Munch et al. (2022).

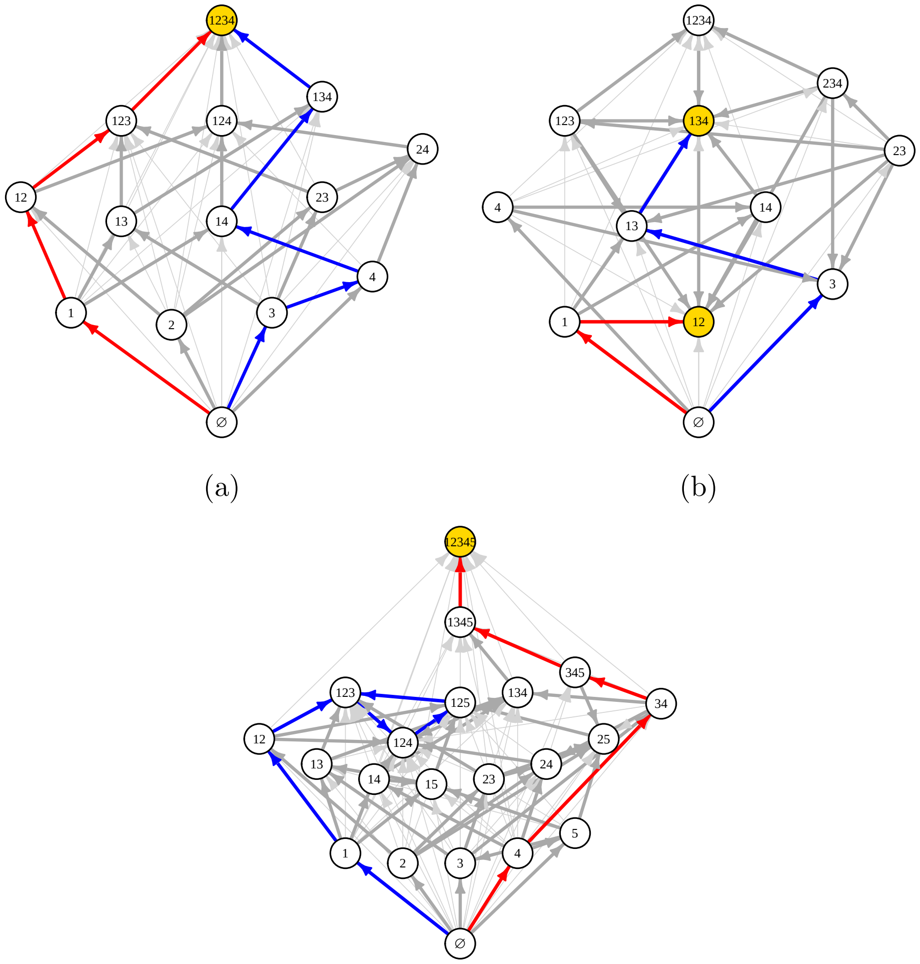
3.2.3 Invasion Growth Rates

Invasion growth rates quantify the average per-capita growth rate of a species when it is relatively rare (termed the "invader"), and the rest of the community is at steady state (termed the "resident"). Intuitively, if the invasion growth rate of a species is positive, the species can increase from rarity and, thereby, escape extinction risk at least in the short term if not in the long-term (Case 1995, Arnoldi et al. 2022). Alternatively, if the invasion growth rate of a species is negative, then once a species reaches low abundance, it would decline to extinction under current conditions. Independently in the mathematical literature, invasion growth rates are used to characterise whether coexistence occurs in the sense of a feasible global attractor (also known as permanence or uniform persistence Hofbauer 1981, Schreiber 2000, Patel and Schreiber 2018). Only recently have the more heuristic approaches in the ecological literature and the rigorous approaches in the mathematical literature begun to merge, providing a unique opportunity to simultaneously evaluate whether coexistence in the sense of permanence occurs in a mathematically rigorous manner, and to probe the mechanisms underlying this coexistence in ecologically meaningful ways.

In practice for coexistence analyses, invasion growth rates are frequently used to understand when two competing species could coexist at a global feasible attractor. Invasion growth rates are quantified for both species, and when both of these invasion growth rates are positive, then each species would increase from rarity and thus they would coexist at a global feasible attractor (Fig. 2e, f). This condition for coexistence is known as the "mutual invasibility" criterion. The mutual invasibility criterion has been used extensively to assess scenarios that yield coexistence and their corresponding mechanisms (Chesson 1994, Adler et al. 2007, Chesson 2018, Barabás et al. 2018, Ellner et al. 2020) (see Section 3.3), and has been extended to communities composed of more than two species by assuming that whenever a species became rare, the remaining species would approach a steady state at which their densities are positive. The invasion growth rate of the rare species would be its average per-capita growth rate at this steady state. Provided that invasion growth rates are positive for all species, coexistence at a global feasible attractor is assumed to occur; as we discuss below, this condition is necessary, but not sufficient for coexistence.

The mutual invasibility framework has several advantages. First, as long as the removal of the species does not incite any co-extinctions of other species, invasion analysis effectively tests whether each species in a community can successfully reestablish itself from low density after being driven locally extinct. For this reason, mutual invasibility is often presented as a more biologically meaningful metric in systems that are subject to strong stochastic influences or frequent large disturbances (Turelli 1981). Indeed, mathematical theory for coexistence in the face of environmental stochasticity relies almost exclusively on this metric (Schreiber et al. 2011, Hening and Nguyen 2018, Benaïm and Schreiber 2019). Second, because mutual invasibility focuses on system dynamics when the focal species is effectively absent from the community, invasion analysis can (at least in theory) ignore feedbacks between the invading species and the rest of the community, which can simplifies mathematical analyses, especially if the total number of species in the community is small.

In empirical studies, invasion rates are often parameterised using data from pairwise competition experiments, where the fitness (e.g. seed production) of individuals of a focal species is evaluated along a density gradient of its competitor (Godoy and Levine 2014, Kraft et al. 2015, Wainwright et al. 2019). However, these pairwise tests are not necessarily indicative of species' performance in diverse communities, e.g. due to effects of intransitive competition, higher-order interactions, or other emergent mechanisms that stabilise (or destabilise) coexistence only under higher diversity and not in pairwise scenarios (May and Leonard 1975, Edwards and Schreiber 2010, Mayfield and Stouffer 2017, Barabás et al. 2018). As such, an increasingly popular alternative approach is to fit models directly to time-series observations of diverse community dynamics (Ovaskainen et al. 2017) or to natural variation in fitness and neighborhood composition across spatial scales (Lanuza et al. 2018). Once parameterised, the model can either be used to estimate invasion rates for each species in the community (Ellner et al. 2020), or fitted parameter values can be compared to formula describing the necessary or sufficient conditions for mutual invasibility in the model (e.g., if species compete more strongly with themselves than each other) (Broekman et al. 2019). Especially popular models for these applications include the Lotka-Volterra competition equations (Chesson 2018) and various augmentations of the Chesson (1990b) annual plant model – though many other models, such as the MacArthur or Tilman resource competition frameworks have also been analysed (Chesson 1990a, Letten et al. 2018). For a more detailed review of these methods, see Grainger et al. (2019), Barabás et al. (2018), and Godwin et al. (2020).



(a) (b)

(c)

Figure 3: Invasion graphs for three empirically parameterised Lotka-Volterra models. Invasion graph (a) is acyclic and as all subcommunities are invadible, the entire community is permanent (gold vertex). Invasion graph (c) is cyclic with all subcommunities invadible, but requires verifying an additional condition (Schreiber 2000) to ensure permanence of the entire community (gold vertex). Invasion graph (b) is acyclic but has two uninvadible subcommunities (gold vertices) which are non-feasible attractors and, consequently, the entire community is not permanent. The vertices in the graphs correspond to steady states of the Lotka-Volterra model and the directed edges correspond to potential community trajectories connecting the steady states as identified by invasion growth rates. Thick edges correspond to transitions due to single species invasions, while thin edges correspond to transitions due to multiple species additions. The colored edges indicate sequences of single species invasions terminating at an attractor for the model.

3.2.3.1 Permanence theory A common critique of coexistence analyses based on invasion growth rates is that, at least superficially, they seem unable to address important nuances of real world systems. For example, how can invasion rates be calculated for predator and prey species, or for obligate mutualists, where the removal of one species necessarily leads to the extinction of the other – or, what of cases where invasions merely lead to subsequent extinctions, such as in "rock-paper-scissors" models (Barabás et al. 2018)?

While in some cases, these concerns have been addressed by model-specific solutions (e.g. Chesson and Kuang 2008, Ke and Wan 2020, Song and Spaak 2024), the mathematical theory of permanence (i.e. a global feasible attractor) provides a general approach for addressing these kinds of questions. While the general abstract mathematical theory was developed in the 1980s (Hutson 1984, Butler et al. 1986, Hofbauer and So 1989) with the connection to invasion growth rates made in 2000 (Schreiber 2000), the theory was too technical for general application in ecology (see, however, Law and Morton 1996 who used an important special case of this theory; Hofbauer 1981). To help demystify this theory, Hofbauer and Schreiber (2022) introduced invasion graphs (Fig. 3). These graphs use invasion growth rates to identify all community trajectories that connect non-feasible steady states (i.e. where at least one species is missing from the community). Provided this invasion graph has no cycles (i.e. no rock-paper-scissor like dynamics), coexistence occurs if and only if, for every non-feasible steady state, at least one missing species has a positive invasion growth rate (Fig. 3a). Hence, in the absence of rock-paper-scissor type cycles, the sign of the invasion growth rates fully determines whether coexistence occurs or not. When the invasion graph, however, has a cycle, one can often use a condition depending on the magnitudes of the invasion growth rates to identify whether the cycle is repelling (Hofbauer 1981, Schreiber 2000, Patel and Schreiber 2018) and, consequently, the community has a global feasible attractor (Fig. 3a).

3.2.4 Time to Extinction

Even in transient systems where coexistence is not predicted, co-occurrence of species can still take place over ecologically meaningful timescales (Lewontin and Cohen 1969, Turelli 1980). Time to extinction provides a quantitative measurement of this tendency, with longer time to extinction indicating longer periods of transient coexistence before extinction occurs (Fig. 2g, h). An advantage of this metric is that it can be applied across ecological systems, regardless of its dynamical behaviour – making it especially useful for characterising transient dynamics in which other coexistence metrics do not apply, or in systems where little is known about underlying steady states and attractors.

At least in theory, the timing of extinctions resulting from deterministic dynamics can be forecast exactly as a function of observed system states and dynamics. However, most modelling frameworks require additional considerations – e.g. in dynamical systems models, abundances approach zero asymptotically, such that they come infinitely close to, but never quite reach, extinction. Common solutions to this problem include including an extinction “cut-off” (quasi-extinction) at an arbitrarily small population size, or include a stochastic component when modelling small populations (Holmes et al.

2007). For models where extinctions result from random fluctuations, time to extinction is typically reported in terms of an expected waiting time (i.e. the average time to extinction that might be observed over many repeated trials). How, exactly, stochasticity influences time to extinction depends on how randomness is structured at the level of individuals vs. populations (Kendall and Fox 2003) (see Section 4.1.3 for more details).

Given relatively simple dynamics and strong theoretical assumptions, mean time to extinction can often be computed using both analytical approximations (Lande and Orzack 1988). For more complex systems, it can often be more efficient to estimate time to extinction directly through long-term simulations of a fitted model (van Nes and Scheffer 2004, Schreiber et al. 2023). Simulation-based approaches for studying time to extinction are especially well developed in population ecology, where carefully tuned integrated population models and integral projection models (IPMs) can be applied to accurately forecast population dynamics for well-studied species (Plard et al. 2019). Recently, more general methods have been developed that attempt to make similar forecasts using less data and fewer biological assumptions, e.g. based insights from statistical mechanics (Arani et al. 2021) and delay embedding approaches (Clark et al. 2022).

3.3 Quantifying Mechanisms that Promote Coexistence

While our focus is on methods for detecting whether species coexist, a parallel and highly complementary body of work focuses on explaining mechanisms that promote, or alternatively hinder, coexistence in a given community.

Broadly, mechanisms that promote coexistence allow species to differentiate among one another in their degree of niche overlap, yielding differences in the strength of intra- and interspecific density dependence (Adler et al. 2018, Chase and Leibold 2009). Coexistence mechanisms can arise in a multitude of ways, such as via trait trade-offs among species (e.g. competition-colonization trade offs; Levins and Culver 1971, Yu and Wilson 2001), specilization of natural enemies and pathogens (e.g. Janzen-Connell hypothesis; Janzen 1970, Connell 1971), differences between species in their limiting resources, or partitioning of variable environmental conditions—as described below. Many studies seek to understand both the potential for coexistence, as we focus on here, and the underlying mechanisms that allow for coexistence. While an in-depth review of these mechanisms falls outside of our scope, we briefly highlight several of the prominent literature on mechanisms of coexistence.

Resource-Ratio Hypothesis and Limiting Resources The resource ratio hypothesis, commonly referred to as R^* theory, states that, given a single limiting resource, whichever species can persist at the lower resource equilibrium level (e.g. R^*) will outcompete all other species (MacArthur 1972, Tilman 1980, 1982). Extending to multiple resources, n species can coexist on n resources within a single site if each species has the lowest R^* for a given resource (and arbitrarily many species can coexist given sufficient spatial heterogeneity), suggesting that niche differences in terms of species' limiting resources can promote species coexistence (Tilman 1982). Since its formalization, the resource-ratio hypothesis has been experimentally tested, with strong support for the theory, although mostly in select grassland and phytoplankton systems due to logistical constraints (reviewed in Miller et al. 2005).

Stabilizing and Equalizing Mechanisms Under a given set of environmental conditions, coexistence is promoted when average fitness differences (i.e. equalizing mechanisms) and niche differences (i.e. stabilizing mechanisms) are balanced (Chesson 1990a, 2008, Barabás et al. 2018): if niche differences are small, then coexistence requires that average fitness differences are correspondingly small, otherwise the species with lower fitness will be competitively excluded. Alternatively, when niche differences between species are large, species can coexist even when average fitness differences are large (Adler et al. 2007, Spaak et al. 2023). However, model parameters, such as intra- and inter-specific competition coefficients, contribute to both niche and fitness differences, leading to a complex interdependency between the two mechanisms, and a need to focus on their aggregated, rather than individual, effects (Song et al. 2019).

While the exact formula for determining niche and fitness differences classically depended on the underlying population model and methodological approach (Godoy and Levine 2014, Letten et al. 2017, Spaak et al. 2023), niche differences and fitness differences can be relatively easily quantified for pairs of species, leading to empirical comparisons of mechanisms across species traits (Kraft et al. 2015), phenology (Godoy and Levine 2014), and environmental conditions (Wainwright et al. 2019, Van Dyke et al. 2022). Methods for quantifying these mechanisms have recently been expanded to consider facilitation (Bimler et al. 2018), plant-soil feedbacks (Ke and Wan

2020, Kandlikar et al. 2019, 2021, Ke and Wan 2022), and cross-trophic level interactions (Spaak et al. 2021, Song and Spaak 2024), thus extending beyond the traditional focus on within-trophic level competition.

Spatial and Temporal Environmental Variability Variability in environmental conditions can increase available niche space, promoting coexistence of competing species. This idea dates back decades (MacArthur 1958, Armstrong and McGehee 1980, May and MacArthur 1972, Turelli 1978, Levins 1979), but was formalised into a general mathematical framework by Chesson (1994) for temporal, and (Chesson 2000b) for spatially variable environments. Broadly, environmental variability can promote coexistence, even when fluctuation-independent growth rates may yield competitive exclusion, via multiple mechanisms: (*i*) the storage effect, where species partition environmental variation, and time periods or locations with beneficial environmental conditions correspond with reduced competition; (*ii*) relative non-linearity, where species each experience their maximum average growth rate at different levels of a fluctuating environmental factor; and (*iii*) growth-density covariance (which only applies for spatial variation), which promotes coexistence if species aggregate in regions where they have high growth rates (Chesson 2000a, 2018, Barabás et al. 2018, Ellner et al. 2019).

A recent simulation-based approach allows for alternative formalisation of mechanisms that promote coexistence under variable conditions, in essence by simulating invasion growth rates for each species under scenarios where spatial or temporal structure is disrupted (Ellner et al. 2019). The relative importance and strength of different coexistence mechanisms can then be quantified by comparing invasion rates with and without each structuring aspect (e.g. spatial or temporal heterogeneity), broadly categorizing mechanisms based on resource availability (Letten et al. 2018), environmental-competitive mechanisms (Hallett et al. 2019, 2023, Aoyama et al. 2022), trait differences (Ellner et al. 2019), top-down and bottom-up forces (Shoemaker et al. 2020), or alternative frameworks.

4 Reconciling Theory and Practice

Recent coexistence research has made great strides in developing effective strategies to bring coexistence theory and practical applications into greater harmony. In the following sections, we first discuss key challenges in integrating coexistence theory with empirical tests (Section 4.1). We then present some general guidelines and a recommended workflow for applying the coexistence metrics discussed in Section 3.2 to characterise dynamical behaviour in empirical contexts (Section 4.2). Finally, we end with a brief prospectus, in which we outline ongoing challenges in empirical coexistence research, and suggest potential ways forward (Section 4.3).

4.1 Special Challenges in Empirical Systems

Empirical systems are typically highly complex, diverse, and interconnected across space and time. Moreover, ecologists have limited a priori knowledge about the species, environments, and underlying biological processes that structure real world systems. Consequently, in addition to the theoretical caveats and scope limitations associated with each of the metrics discussed above, empirical systems present several general classes of challenges that must be considered regardless of the metric applied. These challenges are discussed in detail below, and include: (4.1.1) the underlying biology of empirical systems is often poorly understood; (4.1.2) empirical systems tend to be measured with large sampling uncertainty and (4.1.3) are subject to both demographic and environmental stochasticity; (4.1.4) the spatial and temporal scale of empirical observations are usually highly constrained; and (4.1.5) key ecological properties of empirical systems often violate assumptions that are necessary in analysis of theoretical models.

4.1.1 Incomplete Biological Understanding

There is currently no generally agreed upon "standard model" for describing dynamics in ecological systems. All ecological models must, therefore, be thought of as simplified abstractions, which are at best accurate within a limited scope of times, places, and conditions (MacArthur 1970, Levin 1992). The same caveat is inherited by any coexistence metric applied in empirical contexts: coexistence criteria can be tested for particular theoretical models or mechanisms, but there is no guarantee that these insights can be transferred to any given empirical system. Estimates of time to extinction forecasts illustrate this point particularly well. In a theoretical model, average extinction times can usually be estimated either through analytical formula, or by simulation (Lande et al. 1998, Arani et al. 2021, Schreiber et al. 2023). When applied in practice, however, these forecasts can fail for any number of reasons – e.g. because the wrong equations are chosen to represent the system, the model is improperly parameterised, or simply because initial conditions are imperfectly characterised (Auger-Méthé et al. 2016, Plard et al. 2019, Rogers et al. 2022). Moreover, even if model predictions perform well for a particular community and context, there is no guarantee that it will continue to do so for other times, places, and species (Carpenter et al. 2001).

Analogous issues exist for all other coexistence metrics. Parameter sensitivity analyses, for example, usually focus either on the steady states that are implied by a particular theoretical model (Saavedra et al. 2017), or on local approximations of these states expanded around an observed dynamic trajectory (Cenci and Saavedra 2019). Similarly, although eigenvalue-based estimates of asymptotic stability can be calculated with few assumptions about underlying system dynamics or governing equations (Deyle et al. 2016), these estimates are necessarily only accurate around the specific equilibria under consideration. Thus, changes to the system state (e.g. movement away from a fixed-point equilibrium due to large perturbations) or changes to underlying system dynamics (e.g. due to community turnover or environmental variability) will also lead to changes in the corresponding coexistence metrics (Tilman 1982).

At least in theory, analyses of invasion growth rates can be generalised across a wider range of system states than is true for other metrics. Nevertheless, empirical estimates of species invasion rates have been shown to change dramatically across environmental conditions (Matías et al. 2018, Germain et al. 2018, Hallett et al. 2019, Wainwright et al. 2019, Van Dyke et al. 2022). Thus, whether or not a species successfully invades when introduced into a community at low abundance might be indicative of its average invasion rate, or it could simply be a function of the specific conditions that were tested – potentially overlooking the effects of local vs. regional environmental heterogeneity, inter-annual variability, random chance, etc. While these uncertainties can usually be accounted for in analyses, doing so requires making strong theoretical assumptions about underlying dynamics and functional forms (Letten et al. 2017, Spaak et al. 2023, Weiss-Lehman et al. 2022).

4.1.2 Observation and Detection Errors

Empirical observations in ecology are notoriously noisy, leading both to high rates of observation error (e.g. differences between true vs. measured species abundances), and detection errors (i.e. failing to detect species or incorrectly classifying species identities). Both of these kinds of error can have major ramifications for studies of coexistence. Most obviously, detection error can bias estimates of time to extinction, asymptotic return rates, and invasion success (Kindsvater et al. 2018, Dornelas et al. 2019). For example, if a species is classified as going extinct even though it is still present in the community, extinction rates and occurrences will be under-estimated – or, alternatively, if surveys fail to detect small populations where extinction times are faster, then extinction estimates will be too high (Kuczynski et al. 2023). Many methods have been developed to help reduce such biases (Shimadzu et al. 2016), though again, these tend to require large amounts of data, or strong assumptions about species dynamics and error structure.

Even if all species in a community are correctly detected and identified, observation error in abundance estimates can still confound analyses. For example, even small errors in abundance measurements can lead to large biases in model parameters (Bowler et al. 2022), as well as in corresponding estimates of coexistence metrics (Clark and Neuhauser 2018). Particularly strong biases can occur when observation error is large relative to species average abundances. For example, if invasion rates are calculated using ratios, then measurement error can lead to estimates that have no defined mean or variance, which makes them exceedingly difficult to parameterise from empirical data (Marsaglia 2006). Similar problems can occur for any kind of ratio distribution where noise is large relative to the quantity being observed – for example, when estimating interaction coefficients based on species' performance in mixture relative to monoculture (Carrara et al. 2015), or even when calculating estimates of species relative abundance or density.

4.1.3 Environmental and Demographic Stochasticity

Thus far, we have focused on deterministic models of species interactions. However, ecological systems often experience extrinsic and intrinsic noise, known as environmental and demographic stochasticity, respectively (Lande et al. 2003, Schreiber 2017). Environmental stochasticity arises from stochastic fluctuations in demographic rates due to stochastic fluctuations in environmental conditions such temperature, precipitation, or nutrient availability. In contrast, demographic stochasticity arises from populations consisting of a finite and discrete number of individuals whose demographic fates are not perfectly correlated – independent coin flips are determining whether each individual survives, grows, or survives.

Models with environmental stochasticity share many properties with their deterministic analogs (Levins 1979, Chesson and Ellner 1989, Chesson 1994, Schreiber et al. 2011, Hening and Nguyen 2018, Benaïm and Schreiber 2019).

The stochastic analog of a feasible steady states is a feasible statistical equilibrium that describes, in the long-term, the fraction of time spent near any feasible state (Schreiber et al. 2011, Hening and Nguyen 2018, Benaïm and Schreiber 2019). Unlike deterministic models, however, these statistical equilibria are typically stochastic attractors. For example, if environmental stochasticity is added to a Lotka-Volterra model with bistable competitors, there is no “unstable” statistical equilibrium that separates exclusion of one species from another. Instead, any feasible initial state may lead to the loss of either species with positive probability (Schreiber 2021, Hening et al. 2022). The stochastic analog of global feasible steady state is known as stochastic persistence. Invasion growth rates are a key metric for identifying whether stochastic persistence occurs or not (Schreiber et al. 2011, Hening and Nguyen 2018, Benaïm and Schreiber 2019). Indeed, the use of invasion growth rates in coexistence theory stemmed from Chesson's work on the storage effect for models accounting for environmental stochasticity (Chesson and Warner 1981, Chesson 1994).

For models with environmental stochasticity, extinction typically only occurs asymptotically as population densities approach zero exponentially quickly (Hening and Nguyen 2018, Benaïm and Schreiber 2019). Hence, extinction risk is typically measured by introducing a quasi-extinction threshold below which the species is considered effectively extinct (Fieberg and Ellner 2000). In sharp contrast, extinction typically occurs in finite time for models accounting for demographic stochasticity (Schreiber 2017). Hence, coexistence is always transient in models with demographic stochasticity. However, these transients may be exceptionally long and well described by mean-field models which average out the effects of demographic stochasticity. In particular, when a mean field model has a feasible local attractor, the time to extinction increases exponentially with community size (Faure and Schreiber 2014, Schreiber 2017). Hence, extinction risk can often be safely ignored for sufficiently large populations (Schreiber et al. 2023). In contrast, if the mean field models lacks feasible local attractors, impacts of demographic fluctuations mount over time, such that time to extinction can be ecologically relevant even for large populations (Faure and Schreiber 2014, Schreiber et al. 2023).

The simultaneous effects of environmental and demographic stochasticity are complex and only beginning to be understood. For example, even if invasion growth rates are positive for the mean field model averaging out the effects of demographic stochasticity, long-runs of unfavorable environmental conditions can generate negative transients in the per-capita growth rates of rare species. Under these situations, coexistence times only scale as a power function of community size (Ellner et al. 2020, Prodhomme and Strickler 2021). Hence, even communities with large population sizes may be highly vulnerable to extinction. For these situations, positive invasion growth rates can be a poor metric of coexistence times. For example, Dean and Shnerb (2020) and Pande et al. (2020) showed that increasing environmental stochasticity can simultaneously make invasion growth rates more positive yet shorten coexistence times; a similar phenomena occurs in models of competing species with Allee effects (Schreiber et al. 2019).

4.1.4 The Problem of Scale

One of the most pervasive challenges in ecology is that of scale dependence – i.e. that the processes that drive ecological dynamics vary substantially across space, time, and contexts Levin (1992). These cross-scale problems typically manifest in coexistence studies as a result of differences between the scales at which systems are observed and experimentally manipulated, vs. the scales that are most relevant for coexistence (Chesson 2000a). As a simple illustration, consider the random walk model in Fig. 2 (g, h). The relative abundances of species in this model are entirely determined by demographic stochasticity – thus, at the "global" scale (i.e. considering all individuals in the simulation), all but one species will eventually drift to extinction. However, the system can "appear" to be both asymptotically stable and mutually invasible at smaller observational scales due to mass effects (Hubbell 2001, Clark et al. 2019) – perturbations that reduce local species abundances below the global average are counteracted by immigration from outside of the local patch, and perturbations that increase local abundances above the global average are counteracted because immigration from outside the patch is slower than within-patch mortality.

Similar problems arise for many other kinds of ecological processes and coexistence metrics, though the underlying mechanisms are often more difficult to identify and compensate for (Leibold and Chase 2017). For example, invasion analysis can be challenging to implement using field experiments, as most theoretical frameworks require that invasion rates be averaged across the full range of spatial and temporal variability experienced by the community, whereas most experiments are carried out across a limited range of relatively homogeneous spatial replicates over just a few years. Thus, it can be unclear whether results are indicative of real biological phenomena, or whether they reflect the limited range of conditions that were tested (Kraft et al. 2015). Moreover, these problems cannot be alleviated by simply increasing the scale at which observations and experiments are conducted, as observational scales that are too large can also lead to erroneous conclusions about coexistence (Clark et al. 2019). Indeed, it seems likely that different aspects of coexistence (e.g. for different species, or different temporal periods) are driven by processes that act across many different scales, thereby requiring measurements across many different observational scales to accurately capture their effects (MacArthur 1972).

Another challenge for temporal scale is the correct estimation of generation times and effective population sizes (N_e). Understanding these parameters helps in assessing the viability and extinction risk of populations, as they determine the rate of reproduction and genetic diversity, which in turn influence a population's response to disturbances and demographic fluctuations (Jonasson et al. 2022). Incorrect estimates of generation times can have major impacts on long-term forecasts – especially in systems that include demographically structured population dynamics (Leslie 1966, Brussard et al. 1971). Similarly, N_e is particularly important in small or fluctuating populations, where genetic drift and inbreeding can have significant impacts on the long-term persistence of species. Nevertheless, in practice, these impacts are often omitted from models, either due to the technical complexity of including them, or due to a lack of empirical data or proper genetic markers

(Waples and Yokota 2007).

4.1.5 Violations of Theoretical Assumptions

Aspects of real world ecological systems can clash in important ways with common assumptions that are made to simplify theoretical analyses. For example, many empirical systems lack equilibria (DeAngelis and Waterhouse 1987), and some appear to lack any kind of discernible steady state at all (Pimm et al. 2019) – thereby limiting the kinds of coexistence metrics that can be computed. Even in systems that include feasible steady states, complex dynamics can impede efforts to approximate system dynamics using simple models. Different community assembly pathways, for example, have been shown to lead to fundamentally different kinds of dynamical behaviour and long-term steady states (Fukami 2015), potentially requiring many different measurements and augmented models to accurately characterise coexistence dynamics (Letten and Stouffer 2019). Moreover, many routine challenges that arise in empirical studies – e.g. transfer shock during invasion experiments, carryover effects from the environment in which young organisms are reared, or even germination failure or high mortality rates – are, in practice, exceedingly difficult to model or quantify without making resulting analyses intractably complicated.

An additional challenge is that real world systems are often highly diverse – including anywhere from dozens to thousands of species or taxonomic units even at the smallest possible observational scales (Jurburg et al. 2022). For diversity metrics that rely on measurements of species' monoculture performance, pairwise interactions, or invasion growth rates, this high diversity can necessitate impractically large numbers of experimental replicates (but see Song et al. 2022, for a discussion of efficient sampling strategies). In systems that include many feasible local steady states, this problem is magnified, as each of these states might need to be separately assessed as a potential local attractor (Song et al. 2021). And, even when testing for global attractors, high diversity can present a challenge – e.g. even for relatively well-understood classes of dynamical behaviour, building invasion graphs for communities that include more than a few dozen species is technically infeasible given current algorithms and computational performance (Hofbauer and Schreiber 2022, Spaak and Schreiber 2023).

4.2 Suggested Workflow

Below, we describe a potential workflow for matching available coexistence metrics to different empirical contexts. For each step, we reference a corresponding section in this review where more details and relevant citations can be found. Additionally, the general links between dynamical behaviours (Section 3.1), coexistence metrics (Section 3.2), and empirically relevant research questions and data types are summarised in Fig. 4. Recall that these metrics assess *whether* species can coexist, and additional methods are needed to determine *why* coexistence occurs (Section 3.3).

4.2.1 Select Dynamical Behaviours

The first step is to decide which class of dynamical behaviour (or which combination thereof) you wish to focus on. As discussed in Section 3.1, each of these behaviours relates to a distinct definition of coexistence. Existing hypotheses about the kinds of dynamics that are biologically relevant in your system should be a primary determinant of your choice. For example, if there is reason to believe that your system lacks any discernible feasible steady states, then analyses that focus on transient states may be well-suited. Alternatively, if dynamics seem to occur in the vicinity of one or more fixed-point equilibria (or well-defined invariant sets), then analyses of feasible steady states or local attractors may offer a good balance between ease of application and breadth of insight. Finally, if species appear to be able to coexist in the long-term despite large perturbations, but dynamics are highly complex and variable – then global attractors may provide the broadest possible insights about coexistence in your system.

4.2.2 Identify Relevant Metrics

The combination of coexistence metrics and analyses that you need to apply will depend on the classes of dynamical behaviours that you want to assess. Section 3.2 includes a detailed discussion of metrics that can be applied for each class of dynamic behaviour. There is a rough hierarchy to these metrics – e.g. time to extinction can be calculated for almost any kind of system, but provides relatively little information about broader system dynamics, whereas invasion growth rates can, at least in theory, be used to characterise the overall global stability of coexistence in a system, but in exchange require making very strong theoretical assumptions about the processes that govern system dynamics. This hierarchy does not, however, imply that any one metric is “better” or “more desirable” than the rest – rather, each metric simply elucidates a different aspect of system behavior, each of which is relevant for describing different facets of coexistence.

4.2.3 Assess Available Data and Theory

Coexistence metrics differ greatly in the kinds of data, theory, and models that are required to apply them (see details in Section 3.1, and citations to example applications in Table 4). Thus, it may be necessary to constrain the classes of dynamical behavior that you choose to study based on the availability of this information for your system. For example, if you are willing to assume that community dynamics in your system follow the general Lotka-Volterra equations, then applying most coexistence metrics becomes relatively simple – e.g. parameter sensitivity and asymptotic return rates can be computed directly from species interaction coefficients (measured either from time-series data, or from pairwise interaction experiments), and even analysis of global attractors via permanence theory follows a relatively simple, established protocol.

Alternatively, if theory suggests that interactions in the system are more complex – e.g. including Allee effects, non-linear growth responses, or even higher order interactions – then analyses become more complicated, potentially limiting the kinds of behaviour that can be studied, and usually requiring larger quantities and different kinds of data (e.g. from multi-species mixtures). For instance, current structural approaches for assessing parameter sensitivity are generally limited to models that describe species interactions through a series of linear coefficients – and thus, the approaches cannot yet be applied in systems dominated by non-linear interactions, as might arise from "higher-order" interactions, or from some kinds of resource competition (AlAdwani and Saavedra 2022, Buche et al. 2024). At the far extreme, if there are no existing models or theories about the kinds of biological processes that govern community dynamics in your system, then your analyses will necessarily be constrained by available data. For these kinds of systems, flexible data-driven methods such as EDM may be especially useful (see Section 3.2.2.1).

4.2.4 Interpret Your Results

Finally, recall that empirical systems are not interchangeable with theoretical models. As discussed in Section 4.1, many biologically important aspects of empirical systems tend not to be implemented in common classes of theoretical models (e.g. uncertainty in functional forms of biotic interactions, observation error, cross-scale processes, etc), and some aspects are so complex as to preclude tractable model-based representations at all. Consequently, predictions about coexistence will only ever be as reliable as the assumptions that are used to produce them. Given great uncertainty, it may be prudent to apply simpler, less informative coexistence metrics as well as to avoid making unfounded theoretical assumptions. Even given solid theoretical backing, assumptions and underlying models used to assess coexistence should always be clearly articulated along with other research findings. Additionally, wherever possible, predictions should be tested across multiple different models or theoretical frameworks, both to ensure the robustness of results, and to help distinguish among different potential hypotheses about the processes that are driving community dynamics.

4.2.5 Rinse and Repeat

After interpreting your results, you may find that you need to collect more (or different) kinds of data, plan new experiments, develop alternate theoretical models, etc. You may also find that the behaviours and metrics that you initially chose to focus on are not, in fact, those that are most relevant (or most readily testable) in your system. We therefore strongly suggest an iterative approach to studying coexistence – i.e. returning to previous steps as needed to match your theory, data, and practical needs.

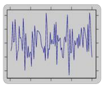
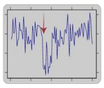
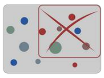
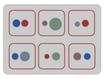
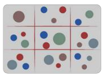
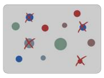
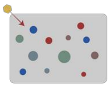
Data type	**Metric**	**Example study descriptions and citations**
Time-series observations		
Time series 	Time to extinction	Fit a stochastic dynamical model to observed time-series of algal dynamics to predict average time to extinction for individual species (Clark *et al.* 2022).
	Parameter sensitivity	Quantified uncertainty in estimates of how strongly species interactions influence community dynamics (Cenci & Saavedra 2018).
	Asymptotic return rate	Used multivariate autoregressive models (MAR) to estimate species interactions and stability properties of naturally varying plankton communities (Ives *et al.* 2003).
Natural disturbance 	Parameter sensitivity	Tracked transient dynamics of an altered marine ecosystem and its current return path towards benthic fish species domination (Frank et al. 2011).
	Asymptotic return rate	Measured multiple stability parameters, including return rates, from vegetation anomalies in remote sensing data (White *et. al.* 2020).
	Invasion growth rate & Asymptotic return rate	Documented average rate of increase when rare, as well as asymptotic divergence rates across spatial replicates, for grassland plant species following agricultural abandonment, based on a century-long chronosequence (Clark *et al.* 2019).
Observations of spatial variation		
	Parameter sensitivity	Computed niche and fitness differences across gradients of pollinators and soil conditions using an annual plant population dynamics model (Lanuza et al. 2018).
	Invasion growth rate	Applied a Bayesian modelling approach to estimate invasion criteria for an annual plant community (Bowler et al. 2022).
Experimental manipulations		
Disturbance 	Parameter sensitivity	Fit a resource competition model to observations of two diatom species grown across a temperature gradient. Simulated models with and without temperature fluctuations to test impacts on coexistence (Descamps-Julien & Gonzalez 2005).
	Asymptotic return rate	Documented the recovery of freshwater microbial communities following experimental mixing of a thermally stratified lake (Shade *et al.* 2012).
Pairwise growth 	Time to extinction	Simulated how third-party species can prolong or shorten competitive outcomes between species pairs (Deng *et al.* 2022).
	Parameter sensitivity	Used density manipulations to estimate interactions between pairs of annual plants, and used those estimates to predict coexistence in communities with more than two species ("geometric projection") (Buche *et al.* 2024).
	Asymptotic return rate	Measured algae species and resource concentrations in monoculture to parametrise resource competition models. Analysed model asymptotic stability characteristics to identify local attractors. Model predictions of coexistence were then tested against empirical observations of two-species mixtures (Tilman 1977).
	Invasion growth rate	Estimating stabilising niche differences and average fitness differences for a pairwise grassland plant competition experiment using an annual plant competition model, and applied the fitted models to predict competitive outcomes (Kraft *et al.* 2015).
Multispecies growth 	Parameter sensitivity	Studied how adding nitrogen and removing leaf pathogens affect the coexistence of species in communities with different numbers of species considering the natural variations in species density and abundance (Granjel *et al.* 2023).
	Asymptotic return rate & Invasion growth rate	Fit resource competition models based on species characteristics measured in grassland monocultures, and analysed model asymptotic stability and invasion rates to identify local and global attractors. Validated predictions of coexistence against experimentally assembled multi-species mixtures (Clark *et al.* 2018).
	Invasion growth rate	Tracked invasion and establishment success of a microbial invader in laboratory microcosms after disturbing (i.e., heat) at different levels (Liu *et al.* 2012).
Knock-outs 	Parameter sensitivity	Removed macroinvertebrate in the sequences in which they are predicted to disappear in response to disturbances and analysed the leaf breakdown rates (Jonsson *et al.* 2002).
	Invasion growth rate	Removed microbial diversity from soil to create a large diversity gradient and tracked the ability of an invader to grow at each point in the gradient (Mallon *et al.* 2015).
Invasion 	Invasion growth rate	A general analytical method that uses both resident community and invader dynamical features to predict whether an invasion causes large long-term impacts on the invaded community (Arnoldi *et al.* 2022).

Figure 4: Caption on next page.

Figure 4: Linking data types and analytical methods for quantifying coexistence in empirical contexts. Rows show different data types and the corresponding metrics (Section 3.2) used to assess coexistence in previous studies. Citations show example applications of each approach, with a short discussion of the work.

4.3 Summary and Outlook

Above all else, we remind readers that it is vital to define coexistence in terms of specific dynamical behaviours and metrics. We recommend that studies specifically state which behaviours and metrics they are applying (e.g. “we analysed asymptotic return rates to test for the existence of a positive local attractor”), facilitating comparisons across studies of coexistence. Similarly, we urge researchers to remain humble and open-minded when interpreting results from coexistence studies. In practice, there is no such thing as single metric that is always right – both because metrics can only test for specific kinds of dynamical behaviour, and because these behaviours describe theoretical abstractions of complex empirical systems. To paraphrase the old adage about models: metrics will always be imperfect, but different metrics are useful under different circumstances.

Given that multiple, mutually inclusive, behaviours can occur in a given system, we suggest that future empirical studies of coexistence move away from single binary tests of whether a particular community can coexist or not, and instead towards applications of a diverse mixture of coexistence metrics. Similar shifts in scope away from individual metrics and towards holistic multidimensional tests have met with much success in general studies of ecological stability, yielding a complementary mix of different kinds of qualitative and quantitative understanding (Donohue et al. 2013, Domínguez-García et al. 2019, Radchuk et al. 2019, Medeiros et al. 2021, Allen-Perkins et al. 2023). It is likely that the same insights apply to coexistence. For example, by quantifying both parameter sensitivity and asymptotic return rates, studies can account for the effect of perturbations on both rate constants (e.g. growth rates, interaction coefficients) and state variables (e.g. species abundances) (Medeiros et al. 2021). Similarly, jointly reporting asymptotic return rates and invasion growth rates within the same study can help show how coexistence is likely to respond to large vs. small perturbations (Clark et al. 2019).

Additionally, we note that a little bit of theory can go a long way – and making a few targeted theoretical assumptions can greatly reduce the scope of empirical data needed to test many coexistence hypotheses. For example, Hallett et al. (2019) used data from rainfall manipulation experiments to parameterise a demographic model – thereby enabling tests of coexistence along a global attractor even with limited spatial and temporal replication. Nevertheless, it is also important to remember that if these *a priori* hypotheses, and corresponding assumptions, are poorly supported, then they can also lead to misleading conclusions. We therefore recommend explicit consideration of these underlying assumptions, and assessment of the robustness of results when assumptions are not met. For example, impacts of demographic stochasticity are often assumed sufficiently small such that they have minimal impacts on invasion success in tests of mutual invisibility. To test the impact of these small effects, Schreiber et al. (2023) reported the probability of invasion success averaged across a large number of replicates. Similarly, West and Shnerb (2022) show that even in highly complex systems, average predictions from a simple comparison of pairwise competition experiments correlated closely (but not perfectly) with those from more complex coexistence criteria. In general, it seems plausible that most classic coexistence metrics will, on average, produce qualitatively similar results when applied to empirical data even if all underlying assumptions are not met – so long as practitioners are careful to acknowledge that these results should be interpreted with care.

Lastly, we stress a balance between building on past hypotheses and equations – which can significantly reduce the data requirements for analyses of coexistence – and testing alternative hypotheses and corresponding equations or even behaviours that might better fit the study system. For example, many studies of grassland coexistence use identical model structure (e.g. Levine and HilleRisLambers 2009, Hallett et al. 2019, Kraft et al. 2015, Van Dyke et al. 2022), facilitating cross study comparison. Simultaneously, however, Terry and Armitage (2024) has noted that using the same model structure repeatedly has impeded inferences of coexistence in some empirical settings, potentially leading to model-specific dependencies of results. To help avoid this problem, combining insight from across multiple different theoretical frameworks (ideally representing multiple different dynamical behaviours and metrics) can help test the generality of results, and facilitate analysis both within and across ecosystems – e.g. by comparing predictions about coexistence across different sets of theoretical assumptions or environmental conditions (Ellner et al. 2019, Walker and Gilbert 2023).

4.3.1 Future Challenges

We believe that a preeminent challenge for coexistence research in the coming years will be the development of new analytical methods that are built hand-in-hand with empirical applications. These new methods need not (and probably should not) seek to define new classes of dynamical behaviour (i.e. Section 3.1) or even new coexistence metrics (3.2) – however, the current generation of methods for matching data to metrics and behaviours has been largely inherited from theoretical studies, and often leave major gaps between theoretical assumptions and practical applications. In particular, these new methods should focus on making testable predictions that can be validated against available data (e.g. "will this species or community persist for the next X years?"), including long-term observations, controlled field experiments, and the growing body of proxy data coming from genetic, trait, and remote sensing studies (Borer et al. 2017, Gonzalez et al. 2023). Moreover, before new methods are introduced to a broader audience, they should be validated extensively against real world data to make their scope and limitations as clear as possible.

Another important next step in coexistence research will be to compare relationships between different coexistence metrics and dynamical behaviours in real world systems. While these relationships are well understood in theory, it is not yet clear how well these theoretical links apply in practice. For example, insights from studies of ecological stability suggest that multivariate relationships across different metrics are often much more constrained in empirical systems than is predicted by theory (Donohue et al. 2013, Radchuk et al. 2019). Interestingly, these constrained relationships could greatly simplify many analyses – e.g. if abundance dynamics for species with very long predicted time to extinction are, in practice, likely to be associated with feasible global attractors, then even relatively "simple" metrics could be used to test for complex dynamical behaviours.

Finally, an enduring challenge for coexistence research is to better match both the spatial and temporal scales at which empirical data are available to the scales that are most relevant for coexistence (Chesson 2000a, Clark et al. 2019). Improving this link is critical under ongoing global change, which challenges many of the assumptions of classic coexistence theory. Strengthening this link will be important for validating new methods, assessing how well our mathematical theory translates to empirical predictions, and thus for using theory to for make predictions that are directly useful for conservation and restoration applications (HilleRisLambers et al. 2012, Hallett et al. 2023). Additionally, more general scaling approaches will be critical for identifying the spatial, temporal, and context-based limits to our ability to understand and forecast coexistence – e.g. the maximum time horizons across which predictions about coexistence can be made (Maris et al. 2018, Tredennick et al. 2021).

4.4 Conclusions

1. ecological coexistence has historically been described using a wide range of independently developed (and sometimes mutually exclusive) definitions and metrics

2. most kinds of community dynamics fall into one of four classes: feasible steady states, feasible local attractors, feasible global attractors, or transient states
3. these four classes of behaviour can be used to define different aspects of ecological coexistence, and can be identified and tested using well-established theoretical metrics: parameter sensitivity (for feasible steady states), asymptotic return rate (for feasible local attractors), invasion growth rates (for feasible global attractors), and time to extinction (in the case of transient states)
4. empirical systems present special challenges for studying ecological coexistence, e.g. due to incomplete biological understanding, impacts of observation error and stochasticity, the problem of scale, other aspects of real world systems that violate common theoretical assumptions
5. identifying and quantifying ecological coexistence in empirical systems therefore requires careful consideration of the class of dynamic behaviour of interest, the kinds of metrics that can be applied to identify that behaviour, and the breadth of conclusions that can be drawn given available data and theoretical understanding
6. we stress that there is no single "correct" class of behaviour or metric for defining and classifying coexistence – we therefore recommend that future studies take a more holistic approach, e.g. by assessing coexistence across a range of dynamic behaviours and metrics, and carefully articulating their scope and limitations

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6 Author Contributions

ATC planned and wrote the first draft of the review. Sebastian Schreiber (SJS) proposed the structure for organising different classes of dynamical behaviours and metrics, with feedback from ATC and LS. All authors contributed significantly to planning, outlining, and writing the final text of the review, and contributed significantly to revising the text and figures. ATC and LS then significantly revised the text to unify concepts, language, and style across sections. Lead authors for revising individual sections of the text include: GB, OG, and SS (parameter sensitivity); ATC and CK (asymptotic stability and dynamic approaches); SJS (invasion growth rates, permanence, and environmental and demographic stochasticity); LS (section on quantifying mechanisms); and ATC (empirical challenges and workflow). CK designed the framework for Fig. 4 with feedback from ATC, RG, OG, and LH.

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