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The Equilibrium Conundrum

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ABSTRACT

The idea that natural systems tend to be at equilibrium dates back to the origin of the field of ecology and continues to underlie most ecological theory. However, empirical evidence for equilibrium dynamics in nature and in experiments is surprisingly elusive. Here, we address this conundrum by first exploring the history of equilibrium in ecological theory and the evidence for equilibrium dynamics in natural systems. We then search the literature to quantify how empiricists deal with equilibrium in their research and address barriers to integrating the concept of equilibrium into empirical work by providing step-by-step instructions for determining whether a population is at equilibrium. Next, we lay out three ways that equilibrium is embedded in theory, and for each, outline when meeting the equilibrium assumption in empirical tests is critical for scientific inference, and when it may be possible to relax this assumption. And finally, we present concrete steps that empiricists and theoreticians can each take in order to meet in the middle when it comes to equilibrium. We hope that this paper will stimulate new discussions from researchers from across the theory-empirical divide about this longstanding issue.

1 | Introduction

The assumption that biological systems are at equilibrium pervades all corners of ecology, transcending scales of biological organisation and underlying theory describing everything from individuals to populations, communities, and ecosystems (Table 1) (Holling 1973; Connell and Sousa 1983; DeAngelis and Waterhouse 1987; Wu and Loucks 1995; Cuddington 2001). The role of equilibrium in ecology reaches back to the very beginning of the field, when mathematical convenience, a society that viewed nature as in harmony and balance and the adoption of conventions from other scientific fields all contributed to a heavy reliance on equilibrium in early ecological thinking (Holling 1973; Pimm 1991; Wu and Loucks 1995; Cuddington 2001). Since then, the equilibrium assumption has grown along with the field of ecology, becoming the foundation on which we have built theory on virtually every topic, from island biogeography (MacArthur and Wilson 1967) to predator–prey dynamics (Lotka 1926; Volterra 1927), consumer-resource interactions (Tilman 1982), metabolic ecology (Brown et al. 2004), metapopulation dynamics (Levins 1969) and coexistence (Chesson 2000) (Table 1). In short, the equilibrium assumption is deeply embedded in ecological theory and in ecological thinking.

However, a critical part of the scientific process is ensuring that the study systems and empirical methods that we use to test theory actually meet the assumptions of that theory, or,

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Matthew A. Barbour and Rachel M. Germain shared senior authorship.

TABLE 1 | Examples of ecological theories that involve equilibrium in some way. Ecological theory can be any explanation of an ecological phenomenon, but here we focus on theories that involve mathematical models because that is where the assumption of equilibrium tends to manifest most clearly. While the definition of equilibrium used in this paper centers on stationarity (Box 1), there are many ways that equilibrium is present in ecological theory, and here we take a comprehensive approach and include theory based on any type of equilibrium assumption. Theories are ordered by biological scale, from the individual to the ecosystem scale.

Theory	Biological scale	How equilibrium manifests in the theory	References
Optimal Foraging Theory	Individual	A lower level of biological organisation (prey density) is assumed to be at equilibrium (i.e., constant through time) when a predator enters a patch. There is also an implied equilibrium such that the energy gain from remaining in the current patch equals the expected gain from moving to a new patch.	(MacArthur and Pianka 1966)
Metabolic Theory	Individual to Ecosystem	Various types of equilibrium are assumed across multiple scales of biological organisation (e.g., metabolic homeostasis assumed, resource supply assumed to be at equilibrium, total ecosystem biomass assumed to be at equilibrium).	(Brown et al. 2004)
Ecological Stoichiometry Theory	Individual to Ecosystem	The elemental composition of biological systems (organisms, ecosystems) is under some form of homeostatic regulation. Strict homeostatic regulation (e.g., consumer elemental composition is maintained, despite changes in resource elemental composition) and no homeostatic regulation (e.g., consumer elemental composition = resource elemental composition) are two equilibrium boundary cases, and most biological systems exist in the space between.	(Sterner and Elser 2017)
SIR Disease Models	Population	Certain disease states (e.g., endemic and disease-free states) represent special cases of equilibrium in which the numbers of susceptible, infected and removed individuals are each constant.	(Kermack and McKendrick 1927)
Metapopulation Theory	Population	The point of interest at which the response variable (proportion of patches occupied) is quantified when there is an equilibrium between colonisation rate and extinction rate (i.e., they are equal).	(Levins 1969)
Lotka-Volterra Theory of Competition	Community	A lower level of biological organisation (the resource) is assumed to be at equilibrium (i.e., constant through time). There is also an assumed separation of timescales such that the resource density is at equilibrium with the consumer (i.e., the resource is always matching changes in the consumer).	(Lotka 1926) and (Volterra 1927)
Neutral Theory	Community	The point of interest at which the response variable (species richness) is quantified is when there is an equilibrium between speciation rate and global extinction rate (i.e., they are equal).	(Hubbell 2001)
R* Theory	Community	A lower level of biological organisation (the resource) is assumed to be at equilibrium (constant through time).	(Tilman 1982)

(Continues)

TABLE 1 | (Continued)

Theory	Biological scale	How equilibrium manifests in the theory	References
Modern Coexistence Theory	Community	Assuming a fixed environment, the coexistence of two competing species requires that there is an equilibrium that is both stable and feasible (each species' equilibrium population size is above zero). Tests of mutual invasibility (i.e., coexistence) also require that each resident, when at equilibrium, can be invaded by each competitor.	(Chesson 2000)
Theory of Island Biogeography	Community	The point of interest at which the response variable (number of species living on an island) is quantified is when there is an equilibrium between colonisation rate and extinction rate (i.e., they are equal).	(MacArthur and Wilson 1967)
Complexity-Stability Theory	Community	The density of the populations in the community or food web are assumed to be at equilibrium (constant through time).	(May 1972)
Biodiversity Ecosystem Functioning Theory	Community to Ecosystem	A lower level of biological organisation (abundance of each species within a community) is assumed to be at equilibrium (i.e., abundances are constant through time).	(Tilman et al. 1997)
Classic Ecosystem Theory	Ecosystem	Ecosystems that persist reach a climax state of dynamic equilibrium.	(Tansley 1935)
Carbon Cycling Theory	Ecosystem	It is assumed that the amount of carbon in the ocean–atmosphere system is at equilibrium (i.e., the input from geological processes equal the output flux from inorganic and organic carbon burial).	(Berner 2004)

if they don't, assessing the implications of that disconnect. And despite its near ubiquity in theoretical ecology, empirical evidence of equilibrium dynamics in nature is famously hard to come by (DeAngelis and Waterhouse 1987; Wu and Loucks 1995; Price 1999) (Table S1). This disconnect between the prevalence of equilibrium in theory and its scarcity in empirical research arises in part because equilibrium is a complex concept that is defined and quantified in many ways (Box 1, Figure 1). While in this paper we use the term 'equilibrium' to refer to a dynamic equilibrium that exhibits stationarity in the state variable (see Box 1 for our full definition), there is no universally accepted definition of equilibrium in ecology. And to add to this confusion, several closely related concepts are often used interchangeably, including stability, constancy, return rates, population regulation, density-dependence, and carrying capacity (Box 1). In addition, existing methods for assessing equilibrium in experimental and natural systems are often mathematically complex and may not be widely accessible (Wiens 1984; Terborgh 2015; Grainger et al. 2022) (Figure 2, Box 2, Figure 3). Furthermore, demonstrating that a system is at equilibrium can be methodologically challenging, and conclusions about whether a system is at equilibrium will depend strongly on the temporal and spatial scale of observation (Box 1). And finally, deviations from equilibrium in empirical studies are only problematic in some cases, and it is not always clear when meeting this assumption will matter for scientific inference and when it will not (Figure 4). All of this means that empiricists have many conceptual and logistical hurdles when it comes to integrating the equilibrium assumption into their research. This may be why the prevalence of equilibrium in natural systems has rarely been explicitly assessed (Table S1), and why the equilibrium assumption frequently goes unmentioned or untested, even in empirical studies using equilibrium-based theory (Figure 2).

In this paper, we argue that the heavy reliance on equilibrium in theoretical ecology coupled with the lack of evidence for this dynamic in nature and experiments creates a disconnect between theoretical and empirical research. We refer to this as the equilibrium conundrum. This conundrum is caused by two overarching factors that we describe and propose solutions for. On the empirical side, it stems from the difficulty in understanding when the equilibrium assumption needs to be met and how to meet it. On the theoretical side, it stems from a history of deeply ingrained equilibrium thinking that has hindered the development of theoretical methods to explore equilibrium dynamics in empirical systems and the development of accessible and general non-equilibrium theory.

We are not the first to cast a critical eye on our reliance on equilibrium; others have discussed the role of equilibrium in ecology (Connell and Sousa 1983; DeAngelis and Waterhouse 1987; Wu and Loucks 1995; Cuddington 2001), advocated for a departure from equilibrium thinking (Sullivan 1996; Spencer 2020; Oro and Martínez-Abraín 2023; Vollert et al. 2025), and introduced theory focused on non-equilibrium dynamics (Chesson 2017; Hastings et al. 2018; Medeiros et al. 2025; Vollert et al. 2025). What is still lacking, that we hope to provide here, is an accessible synthesis of this topic that bridges both theoretical and empirical perspectives and provides concrete steps that each group of researchers can take. While we don't purport to solve this long-standing issue, we hope that this paper can prompt both theoreticians and empiricists to consider how this conundrum affects their research. To empiricists we ask you to consider as you read: is there evidence that this major underlying assumption of the theory on which you base your research is reflected in the dynamics of the system you use, does it matter for the conclusions you are drawing, and if so, are there ways for you to better test and meet this assumption? For theoreticians we ask: if you believe the evidence presented here and elsewhere that equilibrium may not actually be the default state in natural systems, what can you do to help empiricists test for equilibrium, and are there ways to capture this non-equilibrium reality in the theory that you create? And to both we ask: what are the benefits and drawbacks of meeting closer to the middle when it comes to equilibrium?

To prompt these discussions, we first explore three historical reasons for why equilibrium came to be such a foundational assumption in ecology. We then review the literature to determine how often the prevalence of equilibrium in natural systems is assessed and to quantify the extent to which empirical research using equilibrium-based theories acknowledges, addresses or tests this assumption. Next, we outline three ways that equilibrium appears in ecological theory in order to provide guidance for when it is important to meet the equilibrium assumption and when it may not be critical. Finally, we present concrete suggestions for what empiricists and theoreticians can each do to bridge this divide. Advancing our understanding of the natural world requires that entrenched ideas are regularly brought to light, dusted off, and critically examined, and that is what we aim to do here.

2 | How Did Equilibrium Become So Embedded in Ecology?

2.1 | Historical Context

Ideas are not formed in a vacuum, and the deep foothold that the concepts of balance and equilibrium have in ecological research can be traced back to the historical environment in which the field arose (Kingsland 1995; Cuddington 2001; Simha et al. 2022). Within Western thought, these ideas have religious roots that date back to the ancient Greeks, and that were later adopted by the naturalists of the 17th and 18th centuries, each of whom saw natural systems as existing in a divinely ordained state of order and harmony (Egerton 1973; Cuddington 2001; Simberloff 2014). This set the stage for the idea to take hold as ecology was developing as a scientific field in the 19th and 20th centuries, when early founders of the field including Charles Darwin, Herbert Spencer and Stephen Forbes espoused the belief that outside of human influence, nature exists in a state of balance between constructive and destructive forces (Kingsland 1995; Wu and Loucks 1995; Cuddington 2001; Zimmerman and Cuddington 2007; Simberloff 2014). This view was also reflected in the ideas of the early 20th century that communities and ecosystems tend to reach a climax state and then persist in a state of equilibrium (Clements 1916; Tansley 1935; Eliot 2011). It was then reasserted by a new wave of mathematically inclined ecologists, most notably Robert MacArthur, who emphasised an equilibrium perspective as part of a larger push towards general principles and predictability and away from a view of ecological processes as idiosyncratic and subject to the whims of historical contingencies (Kingsland 1995; Wu and Loucks 1995; Cooper 2001).

While biologists have long challenged the idea of balance in nature and identified patterns that did not fit this worldview (Gleason 1917; Ehrlich and Birch 1967; White 1993; Cooper 2001), the mathematical legacies of the idea and its status as a background assumption underlying ecological research have persisted and evolved into the more mathematically based concepts of stability and equilibrium. And even though most ecologists have now moved away from thinking of nature as in balance and harmony (DeAngelis and Waterhouse 1987; Oro and Martínez-Abraín 2023; Barbara 2024; Sprenger 2024), this is still how nature is often portrayed in popular culture and how it is perceived by ecology students and the broader public (Zimmerman and Cuddington 2007; Ladle and Gillson 2009; Ampatzidis and Ergazaki 2018). This idea remains culturally entrenched, which undoubtedly influences how we as ecologists see and study patterns in nature (Simberloff 2014).

2.2 | Influence From Other Scientific Disciplines and Mathematical Tractability

As ecology grew from a descriptive field into a more quantitative discipline, mathematical theory describing the dynamics of ecological systems began to be developed (Lotka 1926; Volterra 1927). Many early pioneers in theoretical ecology were physicists who used the analytic tools of that field (Lotka 1926; Volterra 1927; Bailey 1931; Holling 1973; Kingsland 1995; Cuddington 2001), and the assumption that matter and energy exist in a state of equilibrium underpins classical thermodynamics, a dominant paradigm at that time (Plischke and Bergersen 1994). This is in part because of the strong evidence for equilibrium dynamics in physics (Plischke and Bergersen 1994), but also because analysing mathematical models at equilibrium is more tractable and straightforward (Holling 1973) and because the analytical methods to determine how a system behaves near equilibrium were already well understood (Cuddington 2001). As a result, many of the theories that formed the foundation of ecology were equilibrium-based, in that their solutions were analysed at the point at which the rate of change over time of the focal entity (often population density) is zero (e.g., (Lotka 1926; Volterra 1927; Bailey 1931; Leslie 1948)). Whether due to convention, tractability, or because it is, in fact, the best representation of the system

BOX 1 | What is equilibrium?

Equilibrium and related terms

There are many definitions of equilibrium and many closely related concepts. In this paper, we use 'equilibrium' to refer to a dynamic equilibrium in which the state variables exhibit stationarity. Breaking this down in an example of a population at equilibrium, the stationarity part indicates that the statistical properties of the 'state variable' (a.k.a response variable) remain constant through time; in our example, the mean population size and the variance around that mean would be constant (Figure 1A). The dynamic part means that while underlying processes that affect the state variable are occurring (e.g., births, deaths and migration), they balance one another over some relevant temporal and spatial scale. While our definition centers on stationarity, this definition of equilibrium can also include dynamics such as constancy, oscillations, cyclical behaviour, limit cycles and chaotic dynamics. Constancy is a narrower definition of equilibrium in which there is no change through time (also referred to as a point equilibrium). This occurs when the rate of change of a system's state (i.e., dN/dt) at every moment in time is equal to zero, and the system has settled into a steady state. Carrying capacity is one specific type of equilibrium, defined as the maximum sustainable population size supported by a given environment (Figure 1A). An oscillating equilibrium is a form of dynamic equilibrium in which the system fluctuates through time in a sustained, bounded pattern; while the population's rate of change (dN/dt) is non-zero at most moments, the statistical properties of the oscillation (e.g., its mean and variance) remain constant over the long term. A limit cycle is an isolated, closed trajectory in phase space, meaning that if the system is perturbed slightly, its trajectory will spiral back towards the cycle. Stable limit cycles are a specific type of oscillating equilibrium that function as an attractor (Figure 1B). Chaotic dynamics are bounded, deterministic, aperiodic dynamics that depend strongly on initial conditions, can be difficult to distinguish from randomness and may be predictable in the short term but not the long term (May 1974; Rogers et al. 2022). Note that a chaotic system can include an equilibrium that the system fluctuates around, and that a system that meets our criteria for being at equilibrium could include chaotic dynamics.

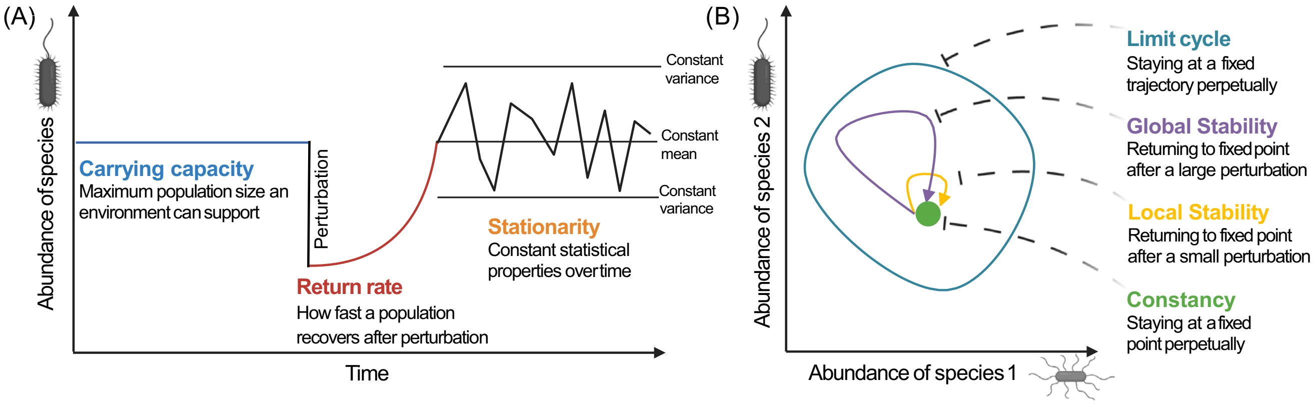

FIGURE 1 | Graphical representation of concepts related to equilibrium. Panel (A) depicts the abundance of a single species (y-axis) over time (x-axis). The initial trajectory (blue line) demonstrates the population at equilibrium (here, carrying capacity). A perturbation then disrupts this equilibrium, causing the population to deviate from its equilibrium state. It then recovers towards its previous equilibrium at a given return rate (red line). The final trajectory (black line) illustrates the concept of stationarity, in which the population fluctuates around a constant mean with constant variance. Panel (B) extends these concepts to two interacting species, illustrating their abundances in a phase space (a graphical representation of the system's possible states, with each axis representing one species' abundance). Focusing on varying perturbation levels at a fixed point reveals different stability states: constancy (no perturbation and no change in the system's state), local stability (robustness to small perturbations) and global stability (robustness to large perturbations). These stability concepts can also be generalised beyond a fixed point.

One common way to think about equilibrium is as a balance between fluxes into a system (e.g., births, resources produced and colonisation) and fluxes out of the system (e.g., deaths, resources consumed, emigration) (Table 1). However, characterising a system as having zero net flux will depend on the spatial and temporal scale of observation; a system that is at equilibrium at one scale may very well be out of equilibrium when the scale changes (DeAngelis and Waterhouse 1987; Simberloff 2014). For example, cycles and stationary dynamics that would not be classified as equilibria on short time scales may settle on a pattern of constant mean and variance that meets our definition of equilibrium if the time scale is long enough. Considering temporal and spatial scale is an integral part of addressing the equilibrium conundrum, and we highlight how empiricists can use scale to find equilibria (in 'What can empiricists do?') and call for theoreticians to develop more approaches to identify the scale of equilibria in natural systems (in 'What can theoreticians do?').

Stability and related terms

Stability is closely related to equilibrium, but they are not equivalent. In broad terms, while equilibrium refers to the presence of some degree of consistency through time in the variable of interest, stability refers to the tendency of a system to return to

(Continues)

BOX 1 | (Continued)

that state when perturbed (Figure 1A,B). While the two concepts are intrinsically linked, stability need not imply the existence of a single equilibrium (e.g., in the case of alternative stable states), and equilibria need not be stable (see below). One common measure of stability is return rate, defined as the rate at which the state variable (e.g., population size) returns to its equilibrium state after being perturbed (Figure 1A). At one end of the stability spectrum is constancy, when there is no change in the system's state (Figure 1B). Moving along the stability continuum, local stability refers to a system that returns to its previous state after infinitesimally small perturbations, while global stability refers to a system that returns to its previous state after a perturbation of any size (Figure 1B). In contrast, an unstable equilibrium is when a system perturbed away from equilibrium moves further from equilibrium, while a neutral equilibrium is when a system perturbed away from equilibrium remains in that new state.

being modelled, this tradition of equilibrium-based theory in ecology has continued ever since, and the bulk of ecological theory developed throughout the 20th and 21st centuries has involved equilibrium in some manner (Table 1).

2.3 | Human Perception and Taxonomic Bias

An additional reason for why scientists and non-scientists alike have readily embraced a view of natural systems as at equilibrium could be that they often appear to be unchanging from a human perspective. As human observers of our natural surroundings, change from one time point to the next can be difficult to detect (Chesson 2017), and while some notable natural phenomena such as pest outbreaks or the extinction of endangered species provide evidence of systems out of equilibrium even to the untrained eye (Holling 1973), these are often viewed as exceptional events rather than the norm. Moreover, recent research has reported that birds and mammals may exhibit more long-term stability than less obvious and charismatic fauna such as plankton and insects (Clark and Luis 2020; Rogers et al. 2022). Humans tend to notice and observe the former taxa more than the latter, and so perhaps the natural world looks more constant to us than it actually is. Finally, there is a tendency for humans to anthropomorphize the world around us, and the idea that nature is self-regulating, self-sustaining, and in balance is a satisfying vision of our world that has been perpetuated in educational settings and in the media (Zimmerman and Cuddington 2007).

2.4 | Is Equilibrium Commonly Observed?

2.4.1 | Equilibrium in Natural Systems

Given the heavy reliance on equilibrium in ecological theory (Table 1), it seems important to assess the evidence for this dynamic in nature (Cooper 2001; Coulson 2021). However, doing so is a challenge. One of the most extensive collective efforts that speaks to this question comes from researchers interested in whether natural systems tend to be stable, regulated and predictable and who have capitalised on large cross-taxa time series datasets of animal populations to answer these questions (Table S1). What is clear from viewing these studies as a group is that their conclusions vary widely. The authors of these studies have found that populations are strongly regulated (Hassell et al. 1976; Thibaut and Connolly 2020), that populations are weakly regulated (Ziebarth et al. 2010; Knape and de Valpine 2012), that chaos is rare (Sibly et al. 2007), that chaos is common (Rogers et al. 2022), and that the degree of stability that populations exhibit depends on taxon (Thibaut and Connolly 2020), body size (Sibly et al. 2007) or generation time (Sæther et al. 2005; Clark and Luis 2020). Moreover, stability, density dependence and population regulation are not the same as equilibrium (see distinctions in Box 1), and we could not identify any cross-taxa analysis that expressly set out to assess how often populations are at equilibrium (e.g., using a method such as the one we propose in Box 2). Furthermore, there are substantial differences in the research questions and approaches of these studies, and it has been demonstrated that the analysis used to assess these dynamics strongly impacts the conclusions drawn (Johnson 2024), which makes it difficult to interpret the results of these studies collectively. In short, all that we can conclude about the prevalence of equilibrium in nature is that it's not often explicitly assessed, and the hints that we have about it from related dynamics remain inconclusive.

Adding further to the inherent difficulty in determining whether or not natural systems tend to be at equilibrium are the widespread and rapid environmental shifts that are occurring as the result of ongoing anthropogenic change (Holling 1973; Chesson 2017). Habitat degradation, nutrification, and urbanisation, as well as changes in temperature and precipitation, are all forces likely to knock even the most equilibrated populations and communities out of this state (Chesson 2017; Newman 2019; Coulson 2021; Vollert et al. 2025). We may therefore now be in an era where equilibrium dynamics are becoming increasingly unlikely. Indeed, evidence that systems are out of equilibrium has been used to demonstrate the influence of global change drivers such as habitat loss (Hanski et al. 1996) and the spread of invasive species (Václavík and Meentemeyer 2012).

In short, the lack of evidence for equilibrium in natural systems, the varied results of studies analysing closely related dynamics, and the intensity of ongoing anthropogenic change all prevent us from confidently asserting that ecological systems tend to be and will continue to be at equilibrium. In light of this, whether or not the individual study systems that we use to test equilibrium-based theory are indeed at (or close to) equilibrium becomes an open question.

2.4.2 | Equilibrium in Experiments

Empirical studies designed to test theories that have an underlying assumption of equilibrium at some scale of biological organisation would ideally include some discussion of this assumption and an attempt to demonstrate that their system is likely to be at or near equilibrium. To determine how empiricists deal with equilibrium, we conducted a Web of Science search on July 24th, 2024, of the top cited articles that test five major equilibrium-based ecological theories: Modern Coexistence Theory, Tilman's Resource Ratio (R*) Theory, the Metabolic Theory of Ecology, Metapopulation Theory, and Neutral theory. We developed search strings iteratively, adding in additional terms specific to each theory (e.g., ‘stabilizing niche differences’ for Modern Coexistence Theory) in order to capture a substantial portion of the literature. Abstracts were screened to verify that the papers involved empirical tests of the theory's predictions, and we retained 10 papers for each theory, for a total of 50 papers (Figure 2).

Out of the 50 articles, 48% stated that there was an assumption of equilibrium in the theory they tested, whereas the remaining articles made no mention of it (Figure 2). Of the papers that acknowledged equilibrium, three papers verbally assumed that their system was at equilibrium (6% of all articles), nine observed that their system or a proxy variable was at equilibrium (18% of all articles), and six cited a violation of equilibrium as a deliberate treatment in their study or an explanation of their results being a poor fit to theoretical models (12% of all articles). There was a group of articles (22%) for which their methodological approach either explicitly or implicitly circumvented the need to demonstrate equilibrium (Figure 4), and some of these papers acknowledged the equilibrium assumption, while others

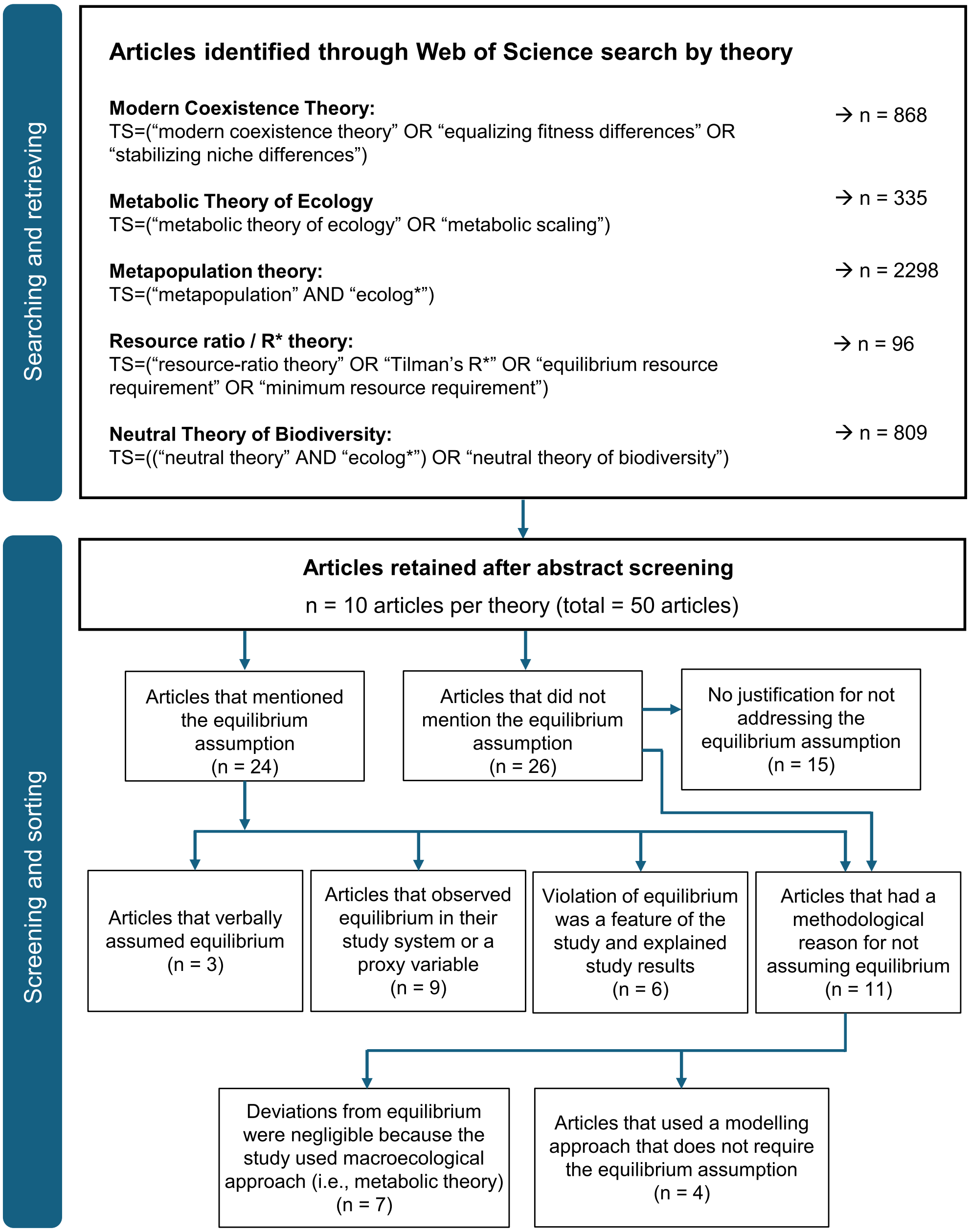

FIGURE 2 | How do empirical studies account for the equilibrium assumption? Flow diagram showing the results of a Web of Science search exploring how empirical tests of ecological theories account for the equilibrium assumption. We developed search strings to capture substantial portions of the literature on five major theories in ecology that invoke an equilibrium assumption. Papers were screened to ensure that they presented new empirical tests of the theory in question, and the top 10 most cited articles within each theory were retained for data extraction. We then identified which articles acknowledged the equilibrium assumption and the steps the authors took (if any) to account for the assumption in their study approach.

did not. Specifically, four studies used a statistical method to estimate equilibrium (e.g., fitting Integral Projection Models to estimate carrying capacity from plant demographic data), while seven studies were macroecological analyses that included data from species spanning taxonomic groups and orders of magnitude of body size, such that deviations from equilibrium are assumed to be negligible compared to large differences among species. Overall, we found a wide variety of approaches in empirical research for addressing the assumption of equilibrium, as well as evidence that empiricists do not always take equilibrium into account. Moreover, it was clear from this review of the literature that empirical tests often do not clearly define the type of equilibrium assumed in the theory they are testing (third column in Table 1), or the biological scale at which it operates (second column in Table 1), both of which are important steps in acknowledging and addressing this assumption. Considering this, we now turn to the question of whether and when not meeting an assumption of equilibrium presents an issue for scientific inference.

2.5 | When Is Not Meeting the Equilibrium Assumption a Problem?

Equilibrium assumptions take on different forms across ecological theories (Table 1), and not meeting them in empirical tests is only problematic when scientific inference relies on them. Even if a theory has an underlying assumption of equilibrium or the predictions being tested come from a model analysed at equilibrium (Table 1), empirical tests of the theory may not always require equilibrium conditions. As such, it is up to the empiricist to determine whether making inferences from data

BOX 2 | Step by step instructions for determining whether a population is at equilibrium.

In this paper, we use 'equilibrium' to refer to a dynamic equilibrium in which the state variables exhibit stationarity (Box 1), and so the central test for whether a system is at equilibrium is whether the statistical properties of the state variable(s) (e.g., mean, variance) will be constant through time. As such, a test of equilibrium by our definition need not employ any specific ecological or mathematical model. However, because ecologists usually view both equilibrium and their data in the context of a mathematical model (Table 1), here we use a method that not only tests for stationarity but also explores equilibrium within a model expression. This method can be applied to any system where the estimated long-term mean of the state variable is positive (e.g., positive equilibrium population abundance).

The first step in our approach is to identify the system's equilibrium by fitting a dynamical model to the observed state variables of the study system (e.g., population abundance). This allows us to then estimate the model's parameters (including the equilibrium value) and their uncertainty. With this information, we then construct 95% credible or confidence intervals around the equilibrium value, which allows us to determine whether the observed state of the system (e.g., abundance at the most recent sampled time point) falls within those confidence intervals. In other words, we test the null hypothesis that the system is at equilibrium—if the observed value falls outside of the confidence intervals, then we reject the null hypothesis and conclude that the system is not at equilibrium.

Below we provide sample code to do this by fitting a discrete-time Gompertz model of flour beetle population dynamics using Bayesian methods. In this example, we grew replicate populations of *Tribolium castaneum* for 11 weeks and counted beetles every 2 weeks, and here we show just three replicate populations from one of our treatments, for simplicity (Weiss et al. unpublished). The discrete-time Gompertz model takes the form (Ives et al. 2003):

$$N_{i,t+1} = r_i + bN_{i,t}$$

where N_t represents the log-abundance of the population in replicate i at time t, r_i is the population's intrinsic growth rate in replicate i, and b is the strength of density-dependence across all replicates. Note that under this parameterization, density-dependence is absent when $b = 1$, and becomes increasingly stronger as b decreases below 1 (Ives et al. 2003). Importantly, r_i and b are equivalent to the intercept and slope estimates of the following auto-regressive model:

```
model_formula <- bf(log(Abundance) ~ 0 + Intercept + log(Abundance_lag1) + (1|ID))
```

We modelled each replicate population as a random intercept (`(1|ID)`), which allows each population to have a different intrinsic growth rate (i.e., r_i) by modelling deviations from the population's mean r (`Intercept`). We then fit a Bayesian hierarchical regression model:

```
brm_model <- brm(formula = model_formula,
                 data = test_df,
                 # priors chosen based on prior predictive checks
                 # and biology of flour beetles
                 prior = c(set_prior(“normal(1,0.5)”, class = b”,
                                coef = “Intercept”),
                           set_prior(“normal(0.5,0.2)”, class = “b”,
                                coef = “logAbundance_lag1”),
                           set_prior(“normal(0,0.2)”, class = “sd”)),
```

(Continues)

```
                    control = list(adapt_delta=0.9), # helped model fitting
                    file = "equilibrium-test") # save the model to make it easier to rerun
```

We chose our priors using prior predictive checks and knowledge of the flour beetle system (see Gabry et al. (2019) for information on how to choose priors). Next, we determined the estimated equilibrium values for each unique replicate (`ID`) of the experiment. The equilibrium population abundance $\widehat{N}$ for each replicate population is given by Ives et al. (2003):

$$\widehat{N}_i = \frac{r_i}{(1 - b)}$$

We then propagated uncertainty from estimates of baseline intrinsic growth rates (`b_Intercept`), deviations from this baseline for each unique replicate (`r_ID`), and the strength of density-dependence (`b_logAbundance_lag1`) to obtain credible intervals (here, 95% and 66% for each parameter) for equilibrium abundances (log scale):

```
equilibrium_summary_stats <- brm_model %>%
  spread_draws(b_Intercept, b_logAbundance_lag1, r_ID[ID,]) %>%
  median_qi(equilibrium_log_scale =
  (b_Intercept+r_ID)/(1-b_logAbundance_lag1),
  .width = c(0.95, 0.66))
```

To confirm whether these populations are at equilibrium, we first tested whether they are stationary. Following Ives et al. (2003), the estimated equilibrium is stationary if $|b| < 1$. We find that the median estimate and its 95% credible interval meet this criteria ($b = 0.74$ [0.62, 0.86]). Next, we visually compared the equilibrium estimates (and credible intervals) inferred from the model to the raw data for each replicate (Figure 3). We can see that the last observed state of the flour beetle populations in all three replicates fall within the credible intervals, and we conclude that there is no evidence that of the populations are outside their equilibrium state.

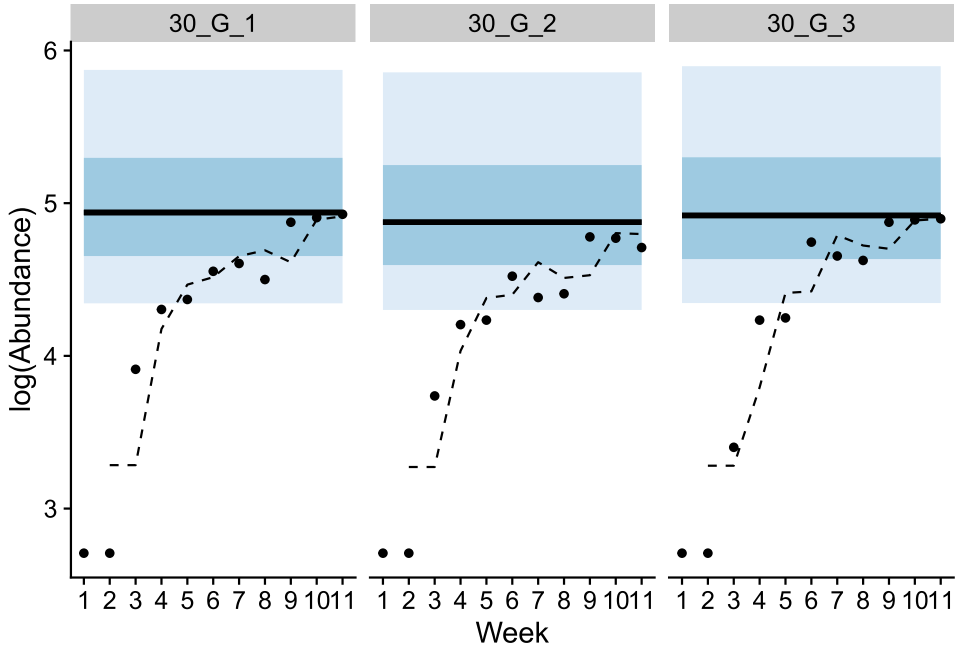

FIGURE 3 | Visualisation of a method to determine whether populations are at equilibrium, applied here to three replicate populations of flour beetles (*Tribolium castaneum*). Points indicate log-abundances of flour beetle populations. Dashed lines represent the population dynamics of the fitted model. Solid lines represent the median estimates of equilibrium population size; dark blue and light blue bands represent 66% and 95% credible intervals of the equilibrium state, respectively.

In this example, we used this method to confirm that the beetle populations had reached equilibrium so that we could test predictions from Metabolic Theory about the effect of temperature on carrying capacity (Weiss et al. unpublished). But this test could be used in any scenario in which it is important to determine that a population has reached equilibrium (Figure 4), including confirming that a resident population is at equilibrium when conducting a mutual invasibility experiment within Modern Coexistence Theory (Narwani et al. 2013; Grainger et al. 2019) or confirming that a population within a habitat patch is at equilibrium in tests of Metapopulation Theory (Hanski and Ovaskainen 2000).

Further information about this method is in the Supporting Information. The full R code to reproduce this analysis is available on GitHub at https://github.com/mabarbour/Equilibrium_conundrum_code and the code has been archived on Zenodo at http://doi.org/10.5281/zenodo.17233205.

collected in systems out of equilibrium is likely to produce incorrect conclusions. Doing so requires understanding the different types of equilibrium assumptions used in different theories. In the following sections, we outline three ways that equilibrium assumptions are invoked in ecological theory and what each means for empirical designs and inference (Figure 4).

2.5.1 | Equilibria When Quantifying Ecological Traits or Characteristics

Many theories used to quantify a metric that tells us something about the ecology of a system assume equilibrium in some way (Table 1). For example, metrics such as niche and fitness differences in Modern Coexistence Theory (Chesson 2000) and R* in Tilman's Resource Ratio theory (Tilman 1982) are quantitative descriptions of species or community traits derived from organisms' performance under static conditions. When used in this way, the equilibrium assumption serves as a useful control to create fair comparisons; we cannot quantitatively compare two species' competitive abilities without those quantities being measured under standardised conditions. However, this does not necessarily mean that the theory only applies to systems at equilibrium. For example, a central aim of many Biodiversity Ecosystem Function (BEF) studies is to understand the relative contributions of complementarity effects (higher diversity causes a release from intraspecific competition and higher exploitation of niche space) versus selection effects (higher diversity means the best performer is more likely to be present) to the BEF relationship. The relative yield total equation ($\mathrm{RYT} = \sum_{i=1}^{n} \frac{N^*}{K}$) quantifies species' performances at equilibrium in monoculture (K) versus polyculture (N^*), and is used to determine whether selection or complementarity effects dominate (Loreau and Hector 2001). However, the theory acknowledges that the relative contribution of selection versus complementarity in a community may vary through time; selection effects may dominate in early stages of community assembly when abundances are low, whereas complementarity effects may dominate in late stages when abundances are higher and more niche space has been filled (Pacala and Tilman 2002). Indeed, there is good evidence of this occurring in plant systems (van Ruijven and Berendse 2005; Huang et al. 2018). Therefore, while the quantitative tools of BEF and related theories do require accurate estimates of equilibrium parameters (here N^* in polyculture and K in monoculture), the theory itself does not exclusively apply to ecosystems at equilibrium. Likewise, while Modern Coexistence Theory requires a resident population to be at equilibrium to accurately measure invasion growth rates (Chesson 2000), in this case a relatively broad definition of equilibrium (e.g., stationary population dynamics) will suffice, and a point equilibrium is not required (Box 1). However, if a resident population is nowhere near equilibrium, then invasion growth rate estimations will be incorrect. And finally, the example given in Box 2 of estimating carrying capacity (a population-level ecological characteristic) in order to test predictions from Metabolic Theory about how temperature affects the maximum individuals a system can support, requires first determining that the populations are indeed at equilibrium. In short, equilibrium must be ensured when estimating an ecological metric that requires it, but a close examination of the theory will be necessary to determine exactly what needs to be at equilibrium and whether a broader definition such as stationary dynamics will suffice to achieve the study objectives (Figure 4).

2.5.2 | Equilibria When Explaining Patterns

One type of equilibrium assumption commonly invoked in macroecological theories such as the Metabolic Theory of Ecology and Maximum Entropy Theory of Ecology is the equivalence or conservation of key ecological quantities such as mass, energy, area or the relative abundances of individuals, populations or size classes. Macroecology seeks to explain highly consistent patterns in the organisation and distribution of ecological systems (Brown 1995), and its theories posit that the statistical regularity with which certain patterns are observed (e.g., species abundance distributions, species-area relationships, scaling laws) must reflect an equilibrium or baseline attractor that ecological systems tend towards (Enquist et al. 2024). For example, the energy equivalence rule (a.k.a. Damuth's Law) posits an inverse relationship between population abundance and body size, such that the total energy flux through populations remains invariant across body sizes within a given area (Damuth 1981). Similarly, the Metabolic Theory of Ecology assumes that the energy required to sustain populations at equilibrium is balanced by a constant resource supply, permitting the derivation of scaling relationships between mass, temperature and equilibrium population abundances (Savage et al. 2004) (Table 1).

A second type of equilibrium assumption in theories that attempt to explain patterns invokes the balance of demographic processes (e.g., births vs. deaths, immigration vs. emigration), as in the Unified Neutral Theory of Biodiversity (Hubbell 2001) and classical metapopulation theory (Levins 1969), both of which build upon the foundations of island biogeography (MacArthur and Wilson 1967). One of the benefits of these simplifying conditions is that they facilitate explanations of general patterns across ecological systems without having to explicitly model the dynamics that produced them.

With both of these types of equilibrium assumptions, the main challenge for empiricists lies in determining whether or not empirical patterns truly reflect equilibrium conditions (Figure 4). In cases where an ecosystem recently experienced a major disturbance, this might be obvious, and in fact, knowledge of the disturbance might present an opportunity to stress test the theory. For example, studies in rocky intertidal communities have found that in spite of known human disturbances affecting species abundances, disturbed communities still follow the inverse size-density scaling predicted by the energy equivalence rule (Marquet et al. 1990; De Boer and Prins 2002). Likewise deviations from theoretical predictions that indicate that a system is not at equilibrium can be informative, for example by indicating that a species is expanding its range (Johnstone and Chapin 2003; Václavík and Meentemeyer 2012), that the system is perturbed and has yet to return to its baseline state (Marquet et al. 1990; Newman et al. 2020) or that strong species interactions or top-down control are structuring a community (McCann et al. 1998). However, when there is no known disturbance or a more

FIGURE 4 | How to determine when breaking the equilibrium assumption is a problem. Whether or not meeting the equilibrium assumption in an empirical test is necessary for scientific inference depends on the research goals and the nature of the equilibrium assumption being made, and empiricists can use this flow diagram to help determine whether they need to ensure equilibrium conditions in their study system, when they should exercise caution in making inferences, and when to pursue alternative non-equilibrium approaches.

general lack of information about past system states, tests of macroecological theories in systems out of equilibrium might lead to incorrect conclusions, such as incorrect estimates of scaling exponents or incorrect inference of niche versus neutral processes. And equations from macroecological theories cannot precisely predict how the state of ecological systems (e.g., population abundances, size distributions and ecosystem fluxes) will change when they are out of equilibrium, or when a new unknown equilibrium has been reached (Stark et al. 2025). When assuming equilibrium to explain patterns, empiricists should carefully consider what is known about their system (e.g., see method in Box 2) and how this informs the interpretation in terms of the theory being tested. If the system meets the equilibrium assumptions of the theory (see examples in Figure 2), then one can make direct inferences based on the theory's predictions. If the system is known to be out of equilibrium, then certain aspects of the theory may still be testable (e.g., inferences about whether macroecological patterns hold under non-equilibrium), but testing questions about specific underlying processes may require additional information (e.g., birth and death rates, resource availability).

2.5.3 | Equilibria When Predicting Future Dynamics

A common goal of ecological research is to use past and current observations to predict the future state or behaviour of ecological systems (Ehrlén and Morris 2015; Fulton et al. 2019), and models with a stable equilibrium are useful when one is interested in a general understanding of future system behaviour. In ecological modelling, equilibria also serve as fundamental reference points for assessing ecosystem stability and resilience in the face of perturbations (Holling 1973; Neubert and Caswell 1997). By solving for the stability properties of equilibria, ecologists can predict the resilience of populations, the persistence of species and the likelihood of regime shifts (Kéfi et al. 2019). One main benefit of using equilibria for this purpose lies in their analytical tractability: stability analyses often yield clear, interpretable conditions under which systems remain within ecological bounds or diverge towards alternative states.

That said, equilibrium assumptions introduce a high risk of incorrect conclusions when frequent perturbations, transient dynamics and nonstationarity dominate system behaviour, and mounting evidence suggests that these processes are common in nature and have significant effects on ecosystem behaviour (Tilman et al. 1994; Scheffer et al. 2009; Stott et al. 2010). Dynamical models of population growth that assume equilibria may not reflect the inherent stochasticity of real ecosystems, rendering equilibrium states elusive or even irrelevant over predictive time frames of interest. Systems that appear to be at equilibrium for long periods of time can undergo sudden and unpredictable changes, a phenomenon termed long transient dynamics (Hastings et al. 2018; Morozov et al. 2020). There are many examples of ecological time series collected in a variety of systems that appeared to exhibit stable or oscillatory equilibria, only to later diverge into unexpected behaviour (Cushing et al. 1998; Jäger et al. 2008; Bruno et al. 2009). If empiricists only measure such a system before they shift, they may erroneously conclude that the system is at an equilibrium (Figure 4). In summary, in order to accurately predict future dynamics, empiricists may need to understand the mechanisms that produce long transients and employ approaches developed to detect transient behaviour (Hastings et al. 2018; Morozov et al. 2020; Barabás 2024) (Figure 4). And given the overall goal of reflecting the realities of natural systems in both theory and empirical work, quantifying the prevalence of long transients and using this to motivate further theory that incorporates these dynamics will be critical (Hastings et al. 2018).

2.6 | What Can We Do About the Equilibrium Conundrum?

With the understanding that equilibrium is widespread in ecological theory, that it cannot be assumed to be ubiquitous in natural systems, and that in certain cases scientific inference may be compromised when the assumption is not met, we now turn to the question of what steps empiricists and theoreticians can each take to address this issue.

2.6.1 | What Can Empiricists Do?

What options are there for empiricists hoping to use theory to make inferences that rely on an assumption of equilibrium (Figure 4)? We describe four potential ways forward (Figure 5): (1) focus empirical applications of equilibrium-based theory on systems that do reach equilibrium, (2) leverage scale to find equilibrium in your system, (3) create an equilibrium experimentally in your system and (4) embrace metrics, statistical methods, and theories that do not rely on equilibrium.

A first option for empiricists wanting to test equilibrium-based theory is to restrict experimental tests to ecological systems for which it is possible to demonstrate equilibrium. Many systems are unlikely to ever be at equilibrium, such as those systems characterised by frequent disturbance (Fukami and Nakajima 2011), transient dynamics (Hastings et al. 2018), or non-cyclical boom-bust population dynamics (Stringer et al. 2024). For empiricists interested in equilibrium-based theories (Table 1), avoiding these experimental systems may be the best path forward (Figure 5A). The benefit of focusing experimental tests of equilibrium-based theory on the subset of ecological systems that do tend to reach equilibrium is that it allows us to more readily meet the assumptions of a huge body of classic theory (Table 1). Furthermore, drawing on research that has looked for equilibrium-adjacent dynamics in natural systems could help guide us towards good candidate systems (Table S1). A drawback of this approach is that it limits the range of experimental systems in which theory can be tested and biases these tests towards systems that may already be over-represented in experiments, such as grasslands and algae (Tilman and Wedin 1991; Hanski and Ovaskainen 2000; Interlandi and Kilham 2001; Narwani et al. 2013). Insofar as the ultimate aim of testing theory is to understand natural systems, restricting tests to certain systems can undermine that aim.

A second option for meeting the equilibrium assumption in experiments is recognising that whether a system is at equilibrium depends entirely on the scale (temporal, spatial and biological) at which the study is conducted (see discussion in Box 1). This can work to the empiricist's advantage. As an example with spatial scale, organisms that live in habitat patches and regularly undergo local extinctions (e.g., aphids on plants, aquatic organisms in ephemeral ponds) can exhibit boom-bust type dynamics on the local spatial scale, and so may not be ideal for testing theory with a local-scale equilibrium assumption, such as Metabolic Theory or consumer-resource theory (Figure 5B). However, they may very well be at equilibrium at the regional scale of many patches if local extinctions are balanced by the regular colonisation of new patches, and could thus be well-suited to testing theory with a regional-scale equilibrium assumption such as metapopulation theory and some branches of Modern Coexistence Theory. Conversely, decreasing the spatial scale through which a system is viewed in order to exclude the processes of colonisation, extinction and range shifts can also make equilibrium more likely, if, for example, those broader-scale processes result in long slow directional shifts towards extinction or extirpation (Yackulic 2017). It may also be possible to explicitly assess the temporal or spatial scale of equilibrium and tailor the scale of an empirical test to match it—for a worked example of how to do this and a call to theoreticians for more simple methods to identify the scale of equilibrium, see section ‘What can theoreticians do?’ below. And likewise, it is important to recognise that theories assume equilibrium at specific biological scale(s) of organisation (Table 1). For example, neutral theory assumes an equilibrium at the community scale, but not at the individual or population scales, while the Metabolic Theory of Ecology assumes equilibrium across many biological scales of organisation (second column of Table 1). For those empiricists not inclined to switch systems, a careful consideration of the spatial, temporal and biological scales at which equilibrium occurs in the system, at which equilibrium is embedded in the theory, and at which the research is conducted can provide empiricists with a tool to better meet the equilibrium assumption. At a minimum, an explicit mention or discussion of the type of equilibrium that underlies the theory being tested, and the scales at which it operates (Table 1), would be a helpful first step that is commonly overlooked in empirical studies (Figure 2).

A third option for empiricists is to impose equilibrium dynamics on systems that don't generally reach an equilibrium in nature (Figure 5C). This can often be achieved in a controlled experimental context, for example, by providing continuous resources for longer or more regularly than would occur in

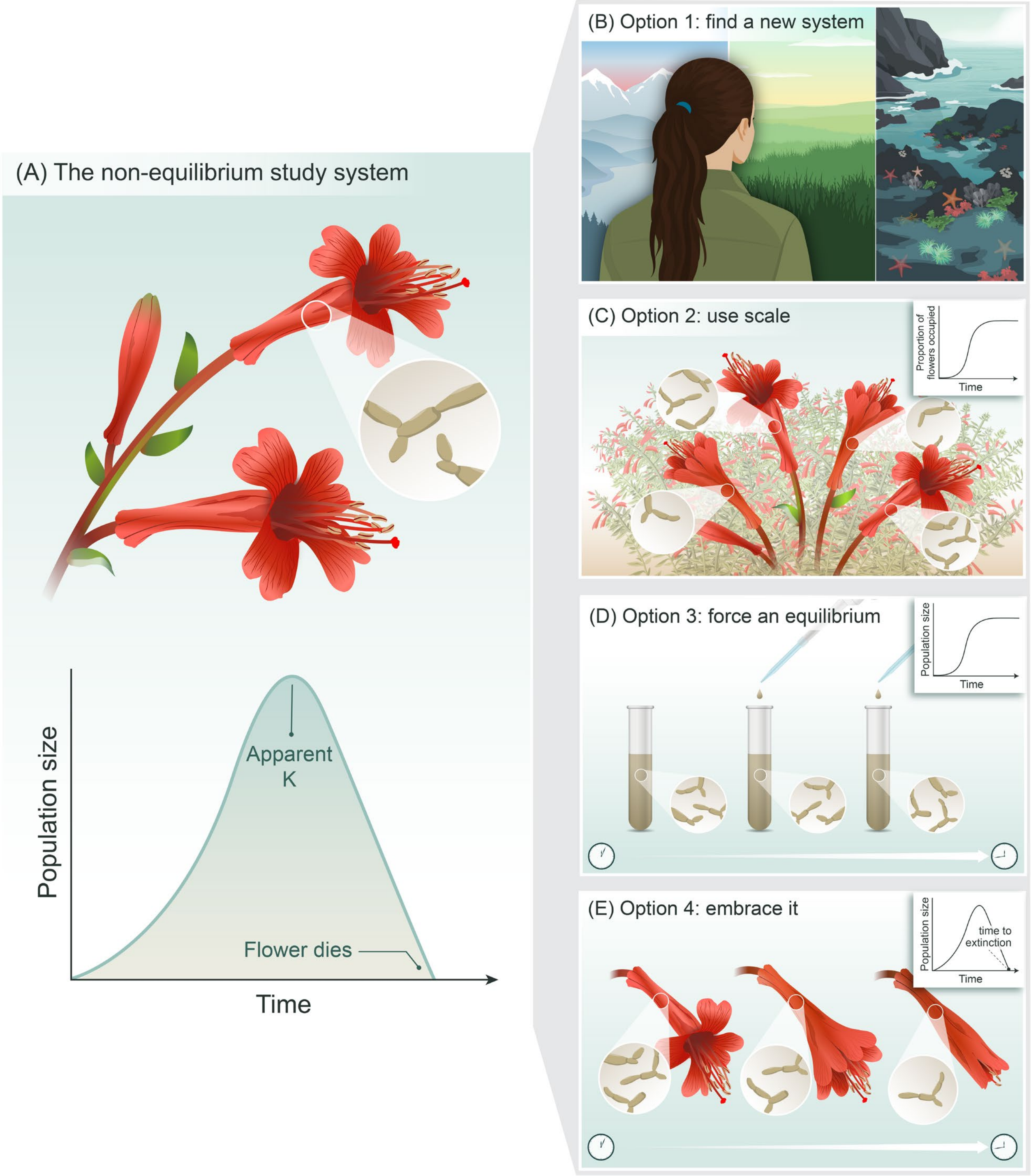

FIGURE 5 | What can empiricists working in non-equilibrium systems do? To illustrate some options that empiricists have when faced with a system that is unlikely to reach equilibrium and when scientific inference is likely to be compromised by not meeting this assumption (Figure 4), we use an example of specialist yeast that inhabit floral nectar and are dispersed by pollinators between plants. While we use this study system as an example, the options outlined below apply to a broad range of systems, in particular those characterised by regular disturbance, an ephemeral habitat, or seasonality. The first step is to (A) determine whether the system reaches an equilibrium, for example by using the method illustrated in Box 2. In some cases it may be obvious that equilibrium is not reached, as in this example where the yeast population within a host flower stops growing (apparent *K*), but this state is only temporary until the host flower begins to senesce. This dynamic is likely to occur in many systems—for example whenever the host dies, the resource is non-renewing, or waste products accumulate. In these cases, (B) the first option is to reconsider if the research question could be better addressed in another system that does reliably reach a stable equilibrium. Alternatively, one could (C) consider whether an equilibrium is reached at some larger spatial or temporal scale (here patch occupancy at a metapopulation scale), for example using the method we outline in the Supporting Information. Or, (D) if the system allows, it might be possible to experimentally create equilibrium conditions, here shown by regularly replenishing resources and using artificial flowers that do not senesce. And finally, (E) one may choose to pivot the response variable of interest towards something compatible with non-equilibrium dynamics, such as time to extinction.

nature. Drawing on the same example systems described above, organisms that normally inhabit ephemeral resource patches in nature have been successfully pushed towards equilibrium in experiments by continuously replenishing the resource and/or substrate, including aphids (Barbour et al. 2022), nectar microbes (Grainger et al. 2019), and aquatic organisms (Srivastava and Lawton 1998). The benefit of this approach is that it broadens the range of study systems available to test equilibrium theory and allows for the use of systems whose characteristics provide useful links to other theories (e.g., food webs (Barbour et al. 2022) and priority effects (Grainger et al. 2019)). The main drawback of this approach is that it provides a less realistic representation of the dynamics of a natural system, and so there is a trade-off to consider between the biological realism of the experiment and its ability to meet assumptions of the theory.

A fourth option for empiricists faced with a system out of equilibrium is to embrace it. One way to do this is to provide evidence that a lack of equilibrium is unlikely to affect the strength of the empirical test or the conclusions drawn, and as described above, a strong case can be made for this in certain situations (Figure 4). Another way to embrace non-equilibrium dynamics is to use departures from equilibrium as a feature of the study. In this way, equilibrium is used as a null model, and evidence indicating that a system deviates from this null expectation can reveal interesting ecological processes. As previously mentioned, many phenomena can cause a departure from equilibrium, including transient dynamics, habitat loss, strong species interactions and spatial dynamics (Marquet et al. 1990; McCann et al. 1998; Johnstone and Chapin 2003). More research on the drivers of non-equilibrium dynamics can provide important insights into the biology of real systems, as well as inform the development of non-equilibrium theories. Following from this, a final way to embrace a lack of equilibrium on the empirical side is by embracing it on the theoretical side as well, by using non-equilibrium theory, metrics and statistical methods. For example, in non-equilibrium systems, one could use metrics that explicitly assume no equilibrium, such as time to extinction (Clark et al. 2024) (Figure 5D). In the following section, we highlight the recent development of explicitly non-equilibrium ecological theories and statistical methods. These ongoing theoretical developments provide an exciting opportunity for empiricists interested in moving away from the equilibrium assumption.

2.6.2 | What Can Theoreticians Do?

What can theoreticians do to help address the equilibrium conundrum? We propose three ways that those comfortable with theory, math, or statistical methods could help bridge the gap: (1) develop tools for assessing the presence of an equilibrium in empirical systems, (2) develop tools for assessing the scale of equilibrium in empirical systems and (3) continue to create more non-equilibrium theory.

One reason for why equilibrium is not always explored in empirical studies may be because doing so can be methodologically challenging and mathematically complex, and empiricists lack clear guidance on how to do it (Grainger et al. 2022). While there has been effort devoted to assessing stability, density dependence, and population regulation in ecological systems (Table S1) and to developing accessible methods to do so (e.g., Ives et al. (2003); Johnson (2024)), there are fewer widely used methods for determining whether or not a system is at equilibrium (see Box 1 for the difference between stability and equilibrium). This is an area in which theoretical developments could help fill the gap. Obviously, any method that tests for equilibrium will depend on the precise definition of equilibrium used, but in cases where the definition of equilibrium centers on stationarity (as ours does), there are existing methods that are commonly used in fields such as economics to test for stationarity (e.g., Augmented Dickey–Fuller test, Kwiatkowski–Phillips–Schmidt–Shin [KPSS] test) that could be more broadly adopted in empirical ecological studies (Lawer 2016; van Dis et al. 2023). Likewise, recent theoretical developments using Empirical Dynamic Modelling (EDM) to assess stationarity in ecological systems are promising (Gee et al. 2023). However, because these methods are not associated with a model expression in the way that most ecologists tend to view their data, they may be less approachable and accessible to a wide range of empiricists. Therefore, in Box 2 we present and provide code for one accessible method that can be used to determine whether equilibrium (by our definition—Box 1) has been reached, and we encourage the development of more accessible methods for assessing equilibrium.

A related problem that could be addressed by theoreticians is the difficulty in determining the spatial and temporal scale at which equilibrium occurs. For instance, on a short time scale, a system might appear to be unchanging, but a longer time series would reveal that it is actually a long transient (Hastings et al. 2018). Or, a system that is not at equilibrium at a small spatial scale may actually be at equilibrium at a larger scale (Figure 4b). Although it is possible to make informed decisions about the scale of observation that will bring the system closer to equilibrium based on natural history knowledge, more could be done on the theory side to develop simple methods for leveraging time series data to identify if a system is at equilibrium at any scale, and if so, what that scale is. As a proof of concept, we lay out one simple approach for how to do this in the Supporting Information, and we call upon theoreticians and computational biologists to build on this idea. Briefly, this approach involves averaging rates of change in a variable of interest (e.g., population size) over a continuum of scales (e.g., windows of time or different spatial extents) in order to identify the scale that yields an average rate of change of 0 (i.e., no net change, an 'equilibrium'). For a predator–prey cycle, for example, such an averaging method would identify as the equilibrium scale the amount of time it takes the system to undergo one full cycle. Employing such a method may not only be of practical interest (i.e., 'how large must my experiment be or how long must I observe it in order to reach equilibrium?') but could also be of biological interest (e.g., 'how and why do equilibrium scales differ among treatments or systems?'). The development of straightforward methods to explore equilibrium in empirical systems such as this one and the one presented in Box 2 (ideally with associated R packages to increase accessibility) would be a valuable contribution towards addressing the equilibrium conundrum.

TABLE 2 | Non-equilibrium dynamics and theories. Examples of non-equilibrium dynamics that occur in natural systems and the theory or approach that can be used to investigate them.

Non-equilibrium dynamic	Example in nature	Non-equilibrium theory or approach
Nonstationarity caused by shifting environments	Systems subject to increasing mean temperatures due to climate change	Asymptotically Environmentally Determined Trajectory (Chesson 2017) DynaMETE (Dynamic Maximum Entropy Theory of Ecology) (Harte et al. 2021) Integrating thermal performance curves over projected temperature distributions (Vasseur et al. 2014; Pinsky et al. 2019; Duffy et al. 2022)
Frequent disturbance caused by external influences	Systems subject to heatwaves, droughts, or wildfires	Non-equilibrium theory focused on the amplification of perturbations (Townley and Hodgson 2008; Medeiros et al. 2025) Equilibrium-free modelling based on ecosystem knowledge (Vollert et al. 2025)
Boom-bust dynamics	Ecological invasions, seasonal insect dynamics	Approaches for assessing boom-bust dynamics, reviewed in Strayer et al. (2017) Bayesian approach for assessing population collapse (Aagaard et al. 2016)
Indeterminate zones	Alternative competitive outcomes that occur by random chance, even with identical starting conditions	Methods for examining the probability distributions of outcomes (Mertz et al. 1976; Dallas et al. 2021)
Long transient dynamics	Insect dynamics prior to outbreaks, extinction debts	Overview of approaches for modelling long transient dynamics in Morozov et al. (2020) Method for analysing the sensitivity of transient dynamics to parameter change (Barabás 2024)

The third way that theoreticians can help address the equilibrium conundrum is by continuing to create theory that does not rely on, or assume, equilibrium (Table 2). Fortunately, there has been an acknowledgement of the limitations of equilibrium approaches and an increase in the introduction of equilibrium-free theories and analytic tools. This includes new approaches to Metabolic Theory of Ecology that are less reliant on steady-state assumptions (Munch et al. 2023; Stark et al. 2025), a focus on theory describing systems subjected to accelerating climate warming (Pinsky et al. 2019; Duffy et al. 2022), and new approaches for predicting regime shifts (Arani et al. 2021; Xu et al. 2023) and responses to extreme climate events (Medeiros et al. 2025). In particular, recent work motivated by ongoing anthropogenic change has focused on approaches that embrace nonstationarity, such as the development of Asymptotic Environmentally Determined Trajectory (AEDT), which allows for the application of a wide range of ecological models to non-stationary systems (Chesson 2017) (Table 2). Likewise the data-driven technique of Empirical Dynamic Modelling (EDM) provides a non-parametric modelling approach that uses machine learning to model nonlinear, state-dependent behaviour directly from data without needing to assume the existence of an equilibrium (Ye et al. 2015). However, creating general and accessible non-equilibrium ecological theory that enjoys broad uptake by empiricists remains an ongoing challenge. This may be because non-equilibrium ecological models are often necessarily mathematically complex, with many of the mathematical concepts used in these theories not taught in ecology courses (Grainger et al. 2022; Ou et al. 2022). But while translating complex math to a broad audience is a perennial challenge across ecology, we encourage continued efforts to increase the accessibility of theory, for example, by explicitly acknowledging the limitations of available data in their approaches (Vollert et al. 2025) and developing tools such as R packages, Shiny apps, and online educational resources aimed at making theory that is broadly accessible and widely adopted.

3 | Conclusion

The disconnect when it comes to equilibrium between how we describe the natural world mathematically (theory), how we study the natural world (empirical research) and how the natural world actually is (nature) is a longstanding issue that we cannot fully resolve here. Rather, we hope that drawing attention to how this issue continues to manifest in our research, and pointing readers towards concrete approaches that we can take to thoroughly examine the assumptions that underlie our research, will lead to more explicit incorporation of the equilibrium assumption in future research. Most importantly, we hope that this piece will spur new discussions and debates as empiricists and theoreticians alike continue to grapple with how to approach and address the complex topic of equilibrium.

Author Contributions

Tess N. Grainger and Rachel M. Germain conceived of the idea for the paper. Chuliang Song created Figure 1, Keila Stark created Figures 2 and 4 and Matthew A. Barbour created Box 2, Figure 3. Tess N. Grainger wrote the manuscript. All authors contributed substantially to revisions.

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Data Availability Statement

The data used to create Figure 1 are available on Dryad (https://doi.org/10.5061/dryad.5hqbzkhgb). The R code and data used in Box 2 are available on GitHub at https://github.com/mabarbour/Equilibrium_conundrum_code and have been archived on Zenodo at http://doi.org/10.5281/zenodo.17233205. The R code used to create the figures for the scale method described in the Supporting Information is available on GitHub at https://github.com/rgerlame/EquilibriumScales and has been archived on Zenodo at http://doi.org/10.5281/zenodo.17238905.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70232.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70232-sup-0001-DataS1.docx.