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SYNTHESIS

# What Have We Learned From Empirical Applications of Modern Coexistence Theory?

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## ABSTRACT

Since the early 2000's, Modern Coexistence Theory (MCT) has guided empirical investigations of coexistence. We reviewed empirical applications of MCT to answer two questions: (1) What have we learned about the strength of temporal, spatial and variation-independent mechanisms of coexistence in nature? (2) How have studies of niche and fitness differences advanced our understanding of coexistence? With respect to the first question, we now have evidence that the temporal storage effect and variation-independent mechanisms help stabilize coexistence in many systems. We have not learned more due to the low number of tests of these mechanisms (24 out of 84 MCT studies), the narrow focus on mechanisms involving temporal variation and grassland communities, and lack of rigorous model validation. With respect to our second question, studies of niche and fitness differences (61 of 84 studies) have answered fundamental questions about the role of phylogenetic relatedness, plant–soil feedbacks, and functional traits in coexistence. We recommend that future empirical MCT studies (1) match hypotheses to MCT quantities, (2) address gaps in empirical studies, (3) avoid known biases in estimating competition coefficients, and (4) validate models with independent data.

## 1 | Introduction

Theoretical ecology has identified many mechanisms that could stabilize species coexistence. How do we determine which ones are strong and which are weak in a natural community? We may suspect, based on the literature, that natural enemies play a critical role in tropical forests while temporal variability is more important in deserts, but how do we quantitatively test this qualitative prediction? Can we use information about the attributes of species and the environment to explain why different coexistence mechanisms are important in different communities? To answer these questions, empiricists must formulate hypotheses about coexistence mechanisms and test them. Although multiple approaches are possible, Modern Coexistence Theory (MCT) is currently the default tool for the job.

MCT refers to the work of Peter Chesson and colleagues to identify and quantify the mechanisms that stabilize coexistence

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in natural communities (P. L. Chesson 1985; P. Chesson 1994, 2000a, 2000b, 2003). Recent studies provide in-depth descriptions of MCT (Barabás et al. 2018; Ellner et al. 2019); here we just emphasize two of its key features. First, it focuses on a quantitative measure of the stability of coexistence. Traditionally, this has been the invasion growth rate, which describes a species' ability to increase from low density when its competitors are near a stochastic steady-state. In a two species system, stable coexistence occurs when both species have positive invasion growth rates, and higher rates are interpreted to indicate more robust coexistence (but see Box 1). Second, MCT relies on counterfactuals to measure the strength of a given mechanism: how much less stable would coexistence be if a particular process or mechanism was prevented from contributing to species' population growth rates? These approaches transformed the study of coexistence from a qualitative effort (i.e., is a given mechanism operating?) to a quantitative effort (i.e., how strong is a given mechanism?). MCT has had a major impact because it allows researchers to connect measurements made in the field to theoretically justified metrics of species coexistence. We focus here on these empirical applications and not the ways MCT has advanced theory.

Over the last two decades, empirical applications of MCT have diverged into two distinct approaches. The first involves partitioning the invasion growth rate into contributions from specific

**BOX 1** | Theoretical limitations.

Like all theories, Modern Coexistence Theory (MCT) relies on assumptions. We argue that for current empirical applications of MCT, these assumptions represent important qualifiers more than barriers.

*Concerns about the invasion criterion*

The invasion criterion is based on the per capita growth rate of a single invader when the resident community is at equilibrium (Turelli 1978; Grainger et al. 2019). This definition has inherent conceptual limitations. First, if species suffer from strong Allee effects, the invasion criteria might fail even if all species could stably coexist once at high abundances (Wang et al. 2011; Barabás et al. 2018; Gil et al. 2019). However, standard MCT applies when Allee effects are too weak to cause a negative invasion growth rate and need only be modified slightly to handle strong Allee effects (Walker and Gilbert 2025).

A second concern is that the invasion growth rate may not reliably predict species persistence times in the presence of strong environmental and demographic stochasticity (Adler and Drake 2008; Yahalom et al. 2019; Pande et al. 2020). Under these conditions, time to extinction or the probability of persistence to some target time may be more appropriate metrics for partitioning. Nonetheless, invasion growth rates are generally informative about persistence times for large systems where demographic stochasticity has little impact (Ellner et al. 2020; Schreiber et al. 2023).

Third, applying the invasion criterion for coexistence to systems with more than two species assumes that, in a system with $N$ species, all communities of $N-1$ species coexist. Fortunately, recent theoretical advances relax this assumption (Hofbauer and Schreiber 2022; Spaak and Schreiber 2023) or partition other coexistence metrics in diverse systems (Saavedra et al. 2017). In addition, qualitative MCT predictions developed to study small communities have proven useful for interpreting the dynamics of very large communities governed by principles of statistical physics (Bunin 2017; Gibbs et al. 2022). Finally, we note that many current MCT applications address diverse systems by focusing on pairwise interactions.

*Concerns about partitioning approaches*

Classical approaches to mechanistic partitioning relying on Taylor expansions of the invasion growth rate describe dynamics near equilibrium with infinitesimal perturbations, whereas natural systems often experience large disturbances. Although simulation-based approaches relax this assumption (Ellner et al. 2016, 2019, 2022), the relative strength of mechanisms may change with perturbation magnitude.

Partitioning inevitably involves investigator decisions about which terms to partition or how to define them. For example, there are multiple ways to decompose the invasion growth rate into niche and fitness differences (Spaak and De Laender 2020) and results may differ depending on the approach (Letten et al. 2017; Spaak et al. 2023). The sense that these decisions are somewhat arbitrary frequently attracts criticism (Barabás et al. 2018), as there is no single 'correct' partition or choice of counterfactual. The question should be: is the choice informative for the hypotheses or questions motivating the study?

*Concerns about the lack of biological mechanisms*

Classic MCT mechanisms like the storage effect or relative nonlinearity focus on the statistical patterns of fluctuation in components of population dynamics (intrinsic growth rates, effects of competition), without reference to the environmental factors and biological processes or traits that generate the patterns. Similarly, estimating niche and fitness differences cannot provide a biological explanation of why species do or do not coexist. The advantage of these MCT approaches is that comparisons are possible across systems with different underlying biological mechanisms. An alternative perspective holds that explaining coexistence in terms of the underlying biological processes and traits is necessary to advance understanding (McPeek 2022; Abrams 2022). MCT can help advance this goal by quantifying stabilizing mechanisms as a first step towards identifying the underlying biological processes or by applying the 'trait decomposition' proposed by Ellner et al. (2019).

*Concerns about modelling positive species interactions*

Recent papers (Simha et al. 2022; James et al. 2025) have criticized applications of MCT that constrained parameters to preclude positive interactions (e.g., Chu and Adler 2015) and argue that coexistence theory itself needs to be modified in order to account for mutualistic and facilitative interactions. However, as long as resident populations are not projected to grow without bound, MCT is already capable of investigating the role of positive interactions in coexistence. New theory shows how to analyse models to quantify the effect of facilitation on coexistence (Ellner et al. 2019) or compute appropriate invasion growth rates even when many subsets of the resident community do not coexist (Hofbauer and Schreiber 2022), as may occur when positive interactions are strong.

mechanisms (P. Chesson 1994; Ellner et al. 2019), such as the temporal storage effect, which motivated the initial development of MCT. This 'mechanistic partitioning' approach answers the central biological question, what are the stabilizing mechanisms that really matter in a community? The second approach involves a coarser partition into niche and fitness differences (e.g., Godoy et al. 2014). The niche difference describes the degree to which a species' growth rate increases when its population falls to very low abundance, buffering that species against extinction. The fitness difference describes a species' average competitive advantage or disadvantage relative to another species in the absence of stabilizing mechanisms. In practice, both of these MCT approaches often, but not always, rely on fitting a competition model to empirical data, and then analytically or numerically computing the coexistence metrics of interest. The niche and fitness difference approach can be implemented with simple, Lotka-Volterra type models of well-mixed systems in constant environments, whereas a mechanistic partitioning may require additional information in the model. For example, information about species' responses to environmental variation would be needed to quantify variation-dependent mechanisms while information about species' responses to predators and pathogens would be needed to quantify the stabilizing effects of natural enemies.

In the early 2000's, the senior authors of this paper were excited about the potential for empirical MCT studies to quantify the mechanisms stabilizing coexistence across a range of natural communities. We thought that achieving this goal would not only answer basic research questions about which processes maintain diversity in different ecosystems (Hutchinson 1959; MacArthur and Levins 1967), but could potentially inform conservation and ecosystem management, since conserving a diversity of species naturally requires maintaining the processes ultimately responsible for their coexistence. Now, a quarter of a century later, we ask: (1) What have we learned about the strength of temporal, spatial, and variation-independent mechanisms of coexistence in nature? (2) How have studies of niche and fitness differences advanced our understanding of coexistence?

Our first step in answering these questions was to review empirical applications of MCT, focusing as much on the questions empiricists tackled and the methods they used as on their results (Section 2). Based on this review, we answer the two questions posed in the previous paragraph (Section 3). In Section 4, we make specific recommendations to improve empirical applications of MCT, before concluding with a broader discussion of the future of MCT (Section 5).

## 2 | Literature Review

To understand how MCT has been used in empirical research, we conducted a literature review. The purpose of the review was to identify the hypotheses and/or coexistence mechanisms investigated in each study, as well as the community type and methodological approach. We were interested in the goal of each study and the MCT approach employed, rather than how well the goal was executed. We address general problems in this population of studies in Sections 3 and 4. We did not conduct a formal meta-analysis of the strength of different coexistence mechanisms given both the technical challenges in comparing results generated using different models and methods as well as our concerns about interpreting model-based results (discussed in Section 3). However, for a few of the most studied individual mechanisms, we collected sufficient case studies to describe patterns in mechanism strength and direction.

### 2.1 | Literature Review Method

To compile a list of candidate papers, on 19 March 2024, using Google Scholar, we applied the following search string to the >7000 papers that cited the foundational MCT paper by P. Chesson (2000a): '("niche difference" OR "fitness difference" OR "invasion growth rate" OR "storage effect" OR "relative nonlinearity")'. The search returned 1230 sources, including unpublished theses and preprints. We compared that list to all papers citing P. Chesson (1994) and did not find any empirical tests missing from our list. After completing our screening and discovering zero empirical studies of fitness-density covariance, we realized we had not included that term in our search string. We conducted an additional search for that term in May 2025 but did not find additional studies. While our list of candidate papers may not include every relevant empirical application of MCT, we are confident it is a sufficient sample to answer our questions about how MCT has been applied in empirical studies.

We screened the list to select studies that truly represented MCT and were empirical. To meet our MCT criteria, studies needed to investigate one or more mechanisms that contribute to the invader growth rates of at least two interacting populations. Studies that met our criteria for *empirical* presented results for a community that existed in a particular place and time (including laboratory settings). Models parameterized with data from various times and places did not qualify.

We then read each study that met our criteria for empirical application of MCT and determined which MCT quantities it evaluated. Our list included niche and fitness differences (defined in Section 1) and the following stabilizing mechanisms (see Table 1 for definitions): any one of the canonical dynamic mechanisms, which include temporal and spatial storage effects, relative nonlinearity of competition, fitness-density covariance, and variation-independent mechanisms, or a specific biological mechanism such as resource partitioning, natural enemies, or facilitation. We collected additional metadata on each study including the community type, whether the study was observational or experimental and carried out in a field or laboratory setting. For field studies, we recorded the latitude and longitude of every study site in each publication and whether the data from each site had been previously used for an MCT analysis. We were able to find geographic coordinates for all sites with the exception of two studies which were re-analyses of previously published studies of niche and fitness differences (Spaak et al. 2021; Spaak and Schreiber 2023).

We included a separate list of subcategories for studies that investigated the factors mediating niche and fitness differences, typically by comparing the strength of niche and fitness differences across experimental treatments or contrasting biotic or abiotic conditions. For example, studies have compared niche and fitness differences under ambient versus reduced rainfall (Van Dyke et al. 2022), with and without competition for pollinators (Johnson et al. 2022),

**TABLE 1** | Definitions of the stabilizing coexistence mechanisms we screened for in our literature reviews. Classic MCT usually lumps the last two mechanisms into the category of variation-independent mechanisms. We screened for them explicitly because current MCT approaches can or have been used to quantify them.

| Mechanism and key reference | Description |
|---|---|
| Temporal storage effect (P. Chesson 1994) | Species-specific responses to temporal environmental fluctuations, combined with a life history that buffers a species against competition when the environment is unfavourable, allows a species that drops to low density to escape competition and benefit greatly from favourable environmental conditions, a benefit not experienced by any species when it is common. |
| Spatial storage effect (P. Chesson 2000b) | Similar to the temporal storage effect, but involves environmental variation in space. In contrast to fitness-density covariance (below), the spatial storage effect does not depend on local aggregation. |
| Fitness-density covariance (P. Chesson 2000b) | Species-specific responses to spatial environmental variation coupled with local dispersal allow species to accumulate in locations favourable to them. |
| Relative nonlinearity of competition (P. Chesson 1994) | Species differences in the non-linearity of their growth response to a temporally fluctuating or spatially varying competitive factor, such as the supply of a limiting resource, favour some species when the limiting factor is highly variable and others when it is nearly constant. Coexistence is promoted when each species alters the variability of the limiting factor in a way that favours its competitor(s). Relative nonlinearity in environmental variables unrelated to competition can also affect invasion growth rates. |
| Variation-independent mechanisms | A catch-all category that includes mechanisms that operate in a spatially and temporally homogeneous environment, such as resource partitioning and natural enemies, along with spatial and temporal environmental variation at scales finer than the sampling unit and time period. Fitness differences are typically implicit in this category. |
| Resource partitioning (Tilman 1982) | When each species in a community is limited by a different resource, then each species will limit its own population growth rate more than it limits other species' growth. These resource-use trade-offs can stabilize coexistence even in a homogeneous environment. |
| Natural enemies (Chesson and Kuang 2008) | Each species is primarily limited by a different combination of predators and pathogens. When a species becomes rare, populations of its specialist enemies decrease, allowing the species to recover. This mechanism can also operate in a homogeneous environment. |

and for pairs of species differing in their phylogenetic relatedness (Narwani et al. 2013) or functional traits (Kraft et al. 2015). We classified these 'niche and fitness difference mediator' studies according to the mediator: environmental factors, natural enemies, facilitation or symbioses, functional traits, plant–soil feedbacks, and natural enemies. After adding these categories, we checked whether any of the mechanistic partitioning studies also considered these mediators.

For studies that involved model fitting, we assessed model validation strategy. We placed each study in one of three classes: No validation, validation using training data, validation with independent data. We did not assess validation for studies that did not rely on models or for studies re-using previously published models.

For mechanistic partitioning studies, we would ideally extract quantitative estimates of the strength of each mechanism. However, due to differences across studies in the units or scalings of population growth rates, we took a qualitative approach and recorded the sign of each mechanism: a positive value contributes to the persistence of a species, a negative value must be overcome by positive contributions from fitness differences or other coexistence mechanisms in order for the species to persist. Thirteen of the 241 observations were recorded as 'zero' effect. When possible, we also recorded the strength of the mechanism relative to the invasion growth rate (i.e., would removing the mechanism change the sign of the invasion growth rate?), and noted whether confidence limits on the estimate of the mechanism, if provided, overlapped zero. We dropped two studies from this analysis (Usinowicz et al. 2012; Zepeda and Martorell 2021) because their results were duplicated within another publication by the same authors included in our review.

We collected sufficient observations to analyse the direction of effect for three coexistence mechanisms: the temporal storage effect, temporal relative nonlinearity of competition, and the net effect of all variation-independent mechanisms. Although we recorded similar observations for temporal relative nonlinearity in the *environment*, we did not analyse them because, due to the lack of a density-dependent feedback, this mechanism cannot stabilize coexistence (no advantage to species when they are rare). For each of the three mechanisms, we fit a generalized linear mixed effects model. The response variable was binary: whether or not the mechanism had a positive effect on the invasion growth rate. The only fixed effect was an intercept, which estimates the probability of observing a positive outcome for each observation. We included study as a random effect to account for non-independence of observations from each publication. We fit the model using the *gam* function in package *mgcv* for R v. 4.3.1 (R Core Team 2023).

We used the estimated fraction of mechanism contributions that were positive to translate from invasion growth rates measured at the level of individual species to an overall effect of a mechanism across communities. Specifically, we took estimated probabilities of a positive contribution significantly greater than 0.5 as evidence that a mechanism is more likely to promote than hinder coexistence. Consider the temporal storage effect: If its true effect is zero, estimated contributions to individual species' invasion growth rates will be positive half the time and negative half the time due to sampling error. For the purpose of this paper, which combines results from many species in many communities, if the storage effect increases the invasion growth rates of more than half the observed species, we will say it stabilizes coexistence. We recognize that this interpretation differs from P. Chesson's (2003) definition of a community average effect. We applied the same null hypothesis to variation-independent mechanisms (which combine variation-independent niche and fitness differences) but for a different reason. Here we took positive contributions greater than 0.5 as evidence for stabilizing niche differences because, in the absence of such mechanisms, the remaining pairwise fitness difference will increase the invasion growth rate of one species and decrease it for the other.

## 2.2 | Results

Of the 1230 search results we screened, 84 studies met our criteria for empirical applications of MCT (Table S1). Twenty-four of these studies (29%) conducted a mechanistic partitioning, 61 (73%) quantified niche and fitness differences, and 2 (2%) computed only fitness differences (Figure 1). Overall, roughly half the studies were conducted in a field setting and half in a lab or greenhouse, and experimental approaches were over four times more common than observational approaches (Figure 2). However, mechanistic partitioning studies were more likely to be conducted in the field than the lab, and nearly as likely to be observational as experimental. By contrast, niche and fitness difference studies were more likely to be conducted in controlled environments using an experimental approach.

Almost half of all studies (49%) were conducted in grassland-type communities or with herbaceous plant species, with lab microcosms and freshwater systems the only other community types or environments represented in more than 10 studies (Figure 1). Of the 41 grassland studies, 33 featured annual plant communities, primarily in Mediterranean ecosystems of California, Spain, and Australia. Despite this concentration, MCT studies are distributed across a variety of biomes and community types, at least in the temperate portion of the northern hemisphere (Figure 3). Furthermore, while some field studies in our collection re-analysed an existing MCT dataset or model, most did not. Of the 69 studies we mapped to specific geographic locations, only 9 were re-analyses.

The 24 mechanistic partitioning studies quantified the following mechanisms (Figure 1): the temporal storage effect (20 studies), the net effect of all variation-independent mechanisms (13), relative nonlinearities in competition or the environment (9), the spatial storage effect (3), natural enemies (2), and facilitative interactions (1). Three of these studies also considered factors that mediate the strength of stabilizing mechanisms. Those factors were functional traits (1), phylogenetic relatedness (1), and temperature (1). Only two studies used community-level metrics (Angert et al. 2009; Li 2016); all other studies quantified mechanisms at the species level.

We further analysed the direction of effects for the three mechanisms quantified in more than three studies. For the temporal storage effect, the probability of a positive effect was 0.69 (95% confidence interval: 0.49–0.84; 90% CI: 0.53–0.82; 94 observations from eight studies; Table S2). Of the 11 observations from eight studies in which the magnitude of the storage effect was large enough to reverse the sign of the invasion growth rate, nine were positive (0.82 probability). For relative nonlinearity of competition, the probability of a positive effect was 0.49 (95% CI: 0.33–0.65; 35 observations from four studies) (Table S3). Within this subset, eight observations from two studies were large enough to reverse the sign of the invasion growth rate, and seven were positive (0.875 probability). For variation-independent mechanisms, the probability of a positive effect was 0.79 (95% CI: 0.62–0.90; 62 observations from 12 studies) (Table S4).

Of the 61 studies that quantified niche and fitness differences, 49 considered one of the following mediators (Figure 1): environmental factors (21), evolution or phylogenetic relatedness (13), plant–soil feedbacks (9), functional traits (5), natural enemies (3), facilitation (2), and other factors (one each for species richness and metacommunity dynamics).

Few model-based studies included rigorous model validation (Table 2). Overall, only 14% validated with training data and 9% validated with independent data. For mechanistic partitioning studies, 36% validated with training data and 10% with independent data. For studies of niche and fitness differences, 5% validated with training data and 10% with independent data. Uncertainty quantification was also rare: of the 22 mechanistic partitioning studies for which we recorded information about mechanisms, 8 provided some measure of uncertainty.

# 3 | Evaluation of Empirical Applications

## 3.1 | What Have We Learned About the Strength of Temporal, Spatial, and Variation-Independent Mechanisms of Coexistence in Nature?

Consistent with the original focus of MCT, ecologists have made substantial progress in understanding coexistence based on temporal environmental fluctuations. Twenty of the studies we reviewed (24%) investigated the temporal storage effect and 13 (15%) examined relative nonlinearity. Based on our review, the temporal storage effect contributed positively to invasion growth rates in 69% of observed cases. In contrast, relative nonlinearity of competition was, on average, as likely to decrease as to increase invasion growth rates (49%), although large effects (relative to the invasion growth rate) were much more likely to be positive (88%). Many of these studies also quantified the role of variation-independent mechanisms as the magnitude of invasion growth rates after contributions from temporal storage

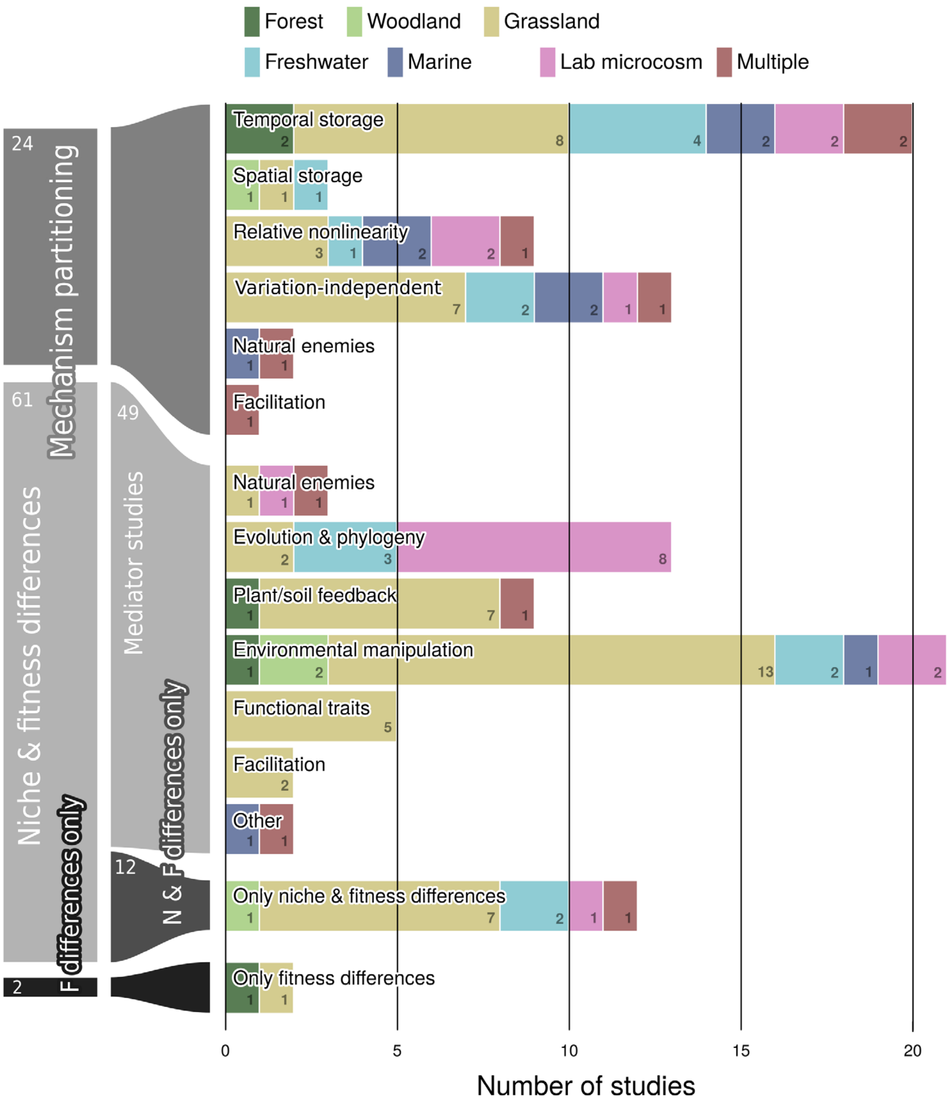

**FIGURE 1** | Empirical applications of MCT studies by purpose and community type. 'Multiple' refers to studies that included more than one community type. Because some studies included both mechanistic partitioning and calculation of niche and/or fitness differences, the total number of studies shown in the three main categories on the left is greater than the number of studies we reviewed (84). 'Mediator studies' investigate biotic and abiotic factors that may explain the strength of niche or fitness differences. While the forest, woodland and grassland studies focus on plants, the freshwater, marine and lab microcosm studies often feature animal communities.

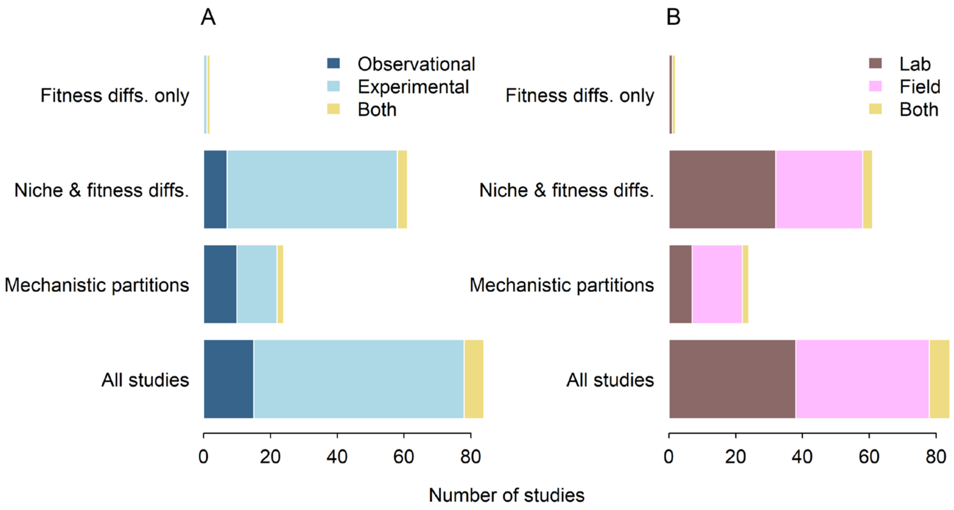

**FIGURE 2** | Methodological approach (A) and physical setting (B) for different subsets (shown on the y-axis) of the 84 studies in the review.

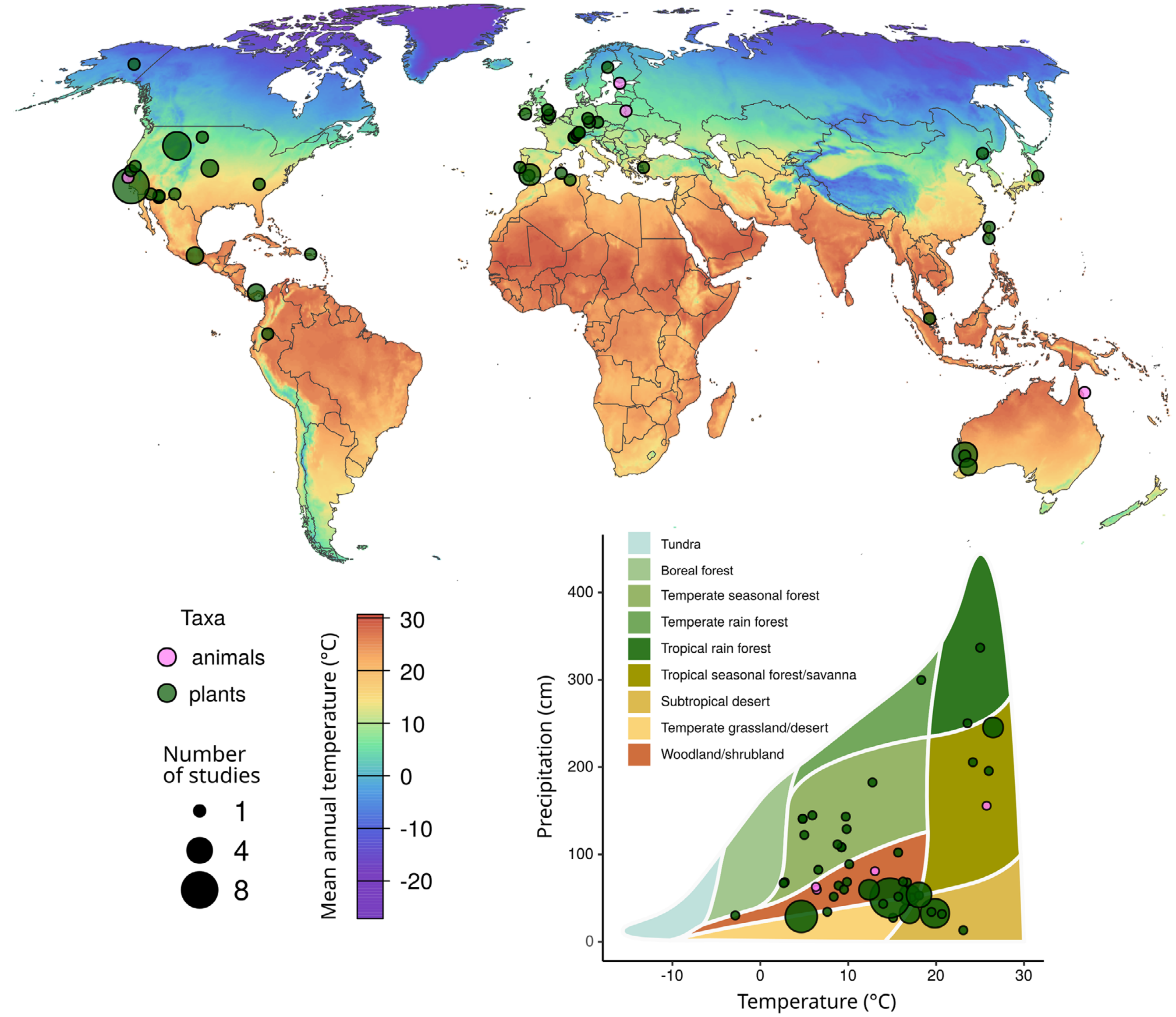

**FIGURE 3** | Locations of 69 field-based MCT studies. Multiple studies at one location may reflect either independent experiments or datasets at the same location or re-analysis of a dataset previously used in an MCT study (9 of the 69).

**TABLE 2** | Model-validation approaches for the 64 studies that involved model-fitting (20 studies did not rely on a model or analysed a previously published model).

| Subset | No validation | Validation with training data | Validation with independent data |
|---|---|---|---|
| All studies | 49 | 9 | 6 |
| Mechanistic partitioning studies | 12 | 7 | 2 |
| Niche and fitness difference studies | 37 | 2 | 4 |

effects and relative nonlinearities were removed. In 79% of these observations, the remaining invasion growth rates were positive. Thus, empirical applications of MCT have provided solid evidence that the temporal storage effect and variation-independent mechanisms, but not relative nonlinearities, are more likely to stabilize than to destabilize coexistence in the communities where they have been studied.

What we have learned is modest relative to the ambitions some of us had 25 years ago. One reason we have not learned more is that the mechanistic partitioning approach has simply not been applied frequently enough for many mechanisms and community types. Our sample of the literature included 24 mechanistic partitioning studies, and only 17 were conducted all or part in field settings. Studies in laboratory and greenhouse environments may be essential for answering basic research questions and testing theory, but they cannot identify the relative importance of mechanisms in specific natural communities. Furthermore, most of the mechanistic partitioning studies focused on the role of temporal environmental variation. This is not surprising, given the initial focus of MCT, but it means we have virtually no information about the role of spatial heterogeneity: only three studies investigated the spatial storage effect, and we found no empirical studies of fitness-density covariance (Table 1), which may be more prevalent than the spatial storage effect (Snyder 2008). In fact, given that fitness-density covariance is the mechanism that best aligns with common intuition about how spatial heterogeneity promotes coexistence (Levin 1974; Mittelbach and McGill 2019, 142–143), it may be the most important single mechanism in many communities. Similarly, while 14 studies quantified the net effect of all variation-independent mechanisms, few studies partitioned that broad category. For example, only two studies examined the role of natural enemies and none applied MCT to investigate resource-use trade-offs. Partitioning these variation-independent mechanisms is now possible using the methods of Ellner et al. (2019). Finally, the existing studies fail to capture a variety of community types. Most studies were conducted in grassland or herbaceous plant communities, with other systems studied only a handful of times or not at all (Figure 1). In summary, with such a low diversity of mechanisms and community types represented, we cannot make general conclusions about the importance of different coexistence mechanisms across a range of natural systems.

The lack of rigorous model validation is a second reason that we have not learned more from empirical mechanistic partitioning studies. When we use a model to quantify the strength of a coexistence mechanism, we assume that the model reasonably approximates nature. The only way to support this assumption is by validating the model. However, our review—which includes many of our own papers—indicates that only one in 10 model-based studies included validation with independent data (Table 2). We expect the results would be similar for most research foci in ecology. Standard practice in our field is to collect data, fit a statistical model, make inferences, then move on to the next study. This workflow may be defensible in the context of traditional linear models which come with well-known checklists of assumptions for inference. But the models we fit to study coexistence are far more complex, often custom-built for each community of interest, and are used for prediction in addition to inference, as when we project long-term population growth rates. Moreover, we know of statistical biases that affect estimates of density-dependence (Freckleton et al. 2006; Detto et al. 2019; Rinella et al. 2020; Xu et al. 2023) and which are difficult to correct. Even more problematic, we use these models to explore boundary conditions, such as a species' growth rate when it falls to low abundance, or counterfactuals, such as dynamics in the absence of temporal variation. Given the current lack of rigorous validation, we simply do not know how much faith to put in the numerical results our models produce. Improving model validation for coexistence research will require clever investments in out-of-sample data for model testing (see Section 4).

### 3.2 | How Have Studies of Niche and Fitness Differences Advanced Our Understanding of Coexistence?

Despite the limitations of mechanistic partitioning studies, empirical MCT research has succeeded in driving progress in directions we could not have anticipated in the early 2000's. Specifically, ecologists have used the coarse-grained decomposition of stabilizing niche differences versus average fitness differences to address classic questions about the determinants of competitive outcomes. Indeed, an early formal use of niche and fitness differences in an empirical context tested the neutral theory of ecology, a framework raising questions about how species differences influence coexistence (Levine and HilleRisLambers 2009). Advances based on quantifying these coexistence metrics were possible because, concerns about uncertainty propagation and model validation notwithstanding, MCT provides theoretically justified, internally consistent, and quantitative measures of stabilizing niche differences and competitive ability. Furthermore, these features of MCT can be exploited with simple models fit to data from short-term experiments.

The flexibility and relative ease of measuring and comparing niche and fitness differences has made the approach popular: of the 84 studies we reviewed, 61 (73%) evaluated niche and fitness differences. Many ecologists now associate MCT with these metrics more than with the storage effect or other variation-dependent mechanisms that motivated the theory. Of the 61 niche and fitness difference studies, 49 (80%) examined factors mediating one or both of these metrics as a way to understand species coexistence more generally. Whereas mechanistic partitioning studies aim to quantify the stabilizing effect of individual mechanisms in units of the invasion growth rate, these studies address conceptual questions about the forces shaping competitive outcomes. They do so by (1) estimating niche and fitness differences for many species pairs and then (2) correlating the niche and fitness differences with other attributes of those communities or pairs, such as evolutionary relatedness, functional trait differences, or plant–soil feedbacks. A separate set of studies examines how environmental variables influence niche and fitness differences. In the rest of this section, we describe how MCT has been used to investigate three commonly studied mediators: evolutionary history, plant–soil feedbacks, and environmental variables.

Thirteen of the 61 (21%) niche and fitness difference studies examined how macro and micro-evolutionary dynamics shape the potential for coexistence between species. This work tests the classic hypotheses, proposed by Darwin, that taxonomic distance predicts the niche differentiation between species as well as their overall competitive imbalance in a given environment. Because these verbal concepts nicely map onto niche and fitness differences, MCT positions investigators to examine how macro and microevolution shape competitive dynamics. Many of these studies have shown that phylogenetic distance maps more strongly onto the fitness differences that drive competitive exclusion than the niche differences that stabilize coexistence (Narwani et al. 2013; Godoy et al. 2014; Hart et al. 2019). This result undercuts a key assumption of phylogenetic community assembly approaches and motivated subsequent papers to explore speciation and character displacement from an MCT perspective (Germain et al. 2021). A similar finding emerged from the four MCT studies that mapped functional trait differences onto niche and fitness differences, with implications for trait-based community assembly.

Eight of the 61 (13%) niche and fitness difference studies explored how plant–soil feedbacks influences species coexistence.

These studies were motivated by early work on plant–soil feedbacks which emphasized the potential for negative feedbacks to stabilize coexistence (Bever 2003). Consistent with that hypothesis, the MCT studies did find that plant–soil feedbacks can lead to stabilizing niche differences. However, they also showed that these interactions often favour one competitor, creating fitness differences large enough to overwhelm the stabilizing niche differences and ultimately lead to competitive exclusion. These empirical applications of MCT question the assumption that plant–soil feedbacks, on balance, promote species coexistence.

Twenty three of the 61 (38%) niche and fitness difference studies tested how niche and fitness differences change with environmental variables, questions motivated by climate change or soil fertility gradients. The studied environmental variables included nutrient availability and temperature, with water availability the subject of the greatest number of studies (9). In contrast to the MCT studies that evaluate how plant–soil feedback or evolutionary relatedness influence species coexistence, these efforts were motivated by questions specific to the environment or ecosystem rather than conceptual problems or common hypotheses (but see Yao and Feng 2022). Given the system-specific motivation, we should not expect general results to emerge across studies. Indeed, for the nine studies examining how water availability affected coexistence, results were highly variable both across studies and across species pairs within each study. For these studies, the application of MCT provided inferences at the level of the study system.

Given that the niche and fitness metrics are too broad to provide much insight into the particular mechanisms impacting coexistence in a given system, the focus on mediators that influence these metrics is natural. The emphasis on general hypotheses about ecological processes contrasts with the mechanistic partitioning approach's focus on system-specific measures of dynamic mechanisms. That said, there are opportunities for merging these two approaches to ask how traits and relatedness shape niche differentiation arising from temporal and spatial variation in the environment. In fact, Angert et al. (2009) and Zepeda and Martorell (2021) do just that, but analogous studies are rare.

## 4 | Recommendations to Improve Empirical Applications

In the process of reviewing the empirical MCT literature, we encountered a common set of problems involving choices of systems and mechanisms to investigate, study design and model building and validation. We offer four recommendations to improve future empirical MCT research. In addition, we refer readers to previous work about the importance of quantifying uncertainty in MCT quantities (Bowler et al. 2022; Yan et al. 2022; Terry and Armitage 2023).

### 4.1 | Ensure the Alignment of MCT Mechanisms With Motivating Hypotheses

MCT is most powerful when an ecological hypothesis involves processes or relationships that closely align with a specific MCT metric. This metric might be the temporal storage effect or the net effect of all stabilizing niche differences. In such cases, MCT provides a theoretically justified metric to quantify the direction and magnitude of a hypothesized mechanism's effect on coexistence. For example, MCT is well suited to evaluating the degree to which interannual rainfall variation promotes species coexistence by generating temporal asynchrony in growth and competition. In this case, quantifying the temporal storage effect, the MCT mechanism invoked by the hypothesis, is the theoretically justified analysis.

By contrast, MCT metrics do not provide an appropriate level of resolution for answering some questions about species coexistence. For example, determining whether a warmer climate promotes or hinders coexistence does not require quantifying niche and fitness differences under different temperatures; it is sufficient to simply evaluate how climate change alters the mutual invasibility criterion or the feasibility of the coexistence equilibrium. In other contexts, the niche and fitness differences are too coarse to be useful. Several of us recently hypothesized that plant species competing for water can coexist via a trade-off between maximum biomass growth rate and tolerance of low soil water (Levine et al. 2022) or, in species competing for light, between high growth rate and reproduction (Detto et al. 2022). We could not empirically test these hypotheses by calculating niche and fitness differences in the field because those metrics do not provide any information about the critical trade-off. In this case, we need a model that explicitly accounts for the physiological differences among species that generate the trade-off. In principle, if such a model were parameterized in the field, the expanded MCT approach of Ellner et al. (2019) could be applied to quantify the trade-off's contributions to coexistence. In sum, MCT is a powerful tool for quantifying sources of species coexistence, but only when the hypothesized mechanism matches the definition and resolution of an MCT metric.

Effectively aligning MCT mechanisms with hypotheses also involves model selection. But selecting the most parsimonious model, as recommended by Terry and Armitage (2023), may sometimes preclude direct tests of hypotheses about the strength of particular mechanisms (Van Dyke et al. 2024). For example, in the process of building a competition model, Chu and Adler (2015) considered including random effects to account for year-to-year variation in competition coefficients. Based on information criteria, they decided not to fit all the year-specific terms. Later, however, they realized that the temporal storage effect could not operate in their model without year-specific competition coefficients (Ellner et al. 2016). The fact that information criteria favoured the simpler model is indirect evidence that the temporal storage effect would be weak. Yet in hindsight, rather than selecting a model that effectively assumes zero storage effect, they should have fit the more complex model and propagated the uncertainty through to the final estimate of the storage effect. Accounting for that uncertainty is important because increasing model complexity can also increase parameter uncertainty. Similar considerations will apply to studies of relative nonlinearity; while information criteria might support selection of a linear over a nonlinear model, the mechanism cannot operate in the linear model.

## 4.2 | Address Gaps in Empirical Case Studies

Existing case studies focus primarily on grasslands (41 of 84) and annual-dominated grasslands in particular (33 of 84). Other natural community types are represented by only a handful of case studies or none at all. The focus on annual grasslands makes sense: the small stature and short lifespans of the dominant species is amenable to experimentation and model-building. In addition, many of the early, precedent-setting applications of MCT were conducted in annual plant communities (Pake and Venable 1995; Sears and Chesson 2007; Angert et al. 2009; Levine and HilleRisLambers 2009). We already have the tools to model communities of organisms with more complex life cycles using long-term observational data (e.g., Adler et al. 2010); the real challenge is conducting meaningful, short-term experiments in these systems. One possibility is to use long-term observational studies to identify the life stage contributing most to coexistence (Chu and Adler 2015) and then design experiments focused on that stage (Chung et al. 2023).

Given the availability of long-term census data for forest communities, why do so few MCT studies feature them? In principle, traditional stage or size structured population models can be fit using short-term data, provided all stages and sizes can be observed. In forests, recruitment events and deaths of canopy trees may be observed too infrequently to support parameter estimation. Complex simulation models trained with both forest inventory data and remotely-sensed observations may provide an alternative. Forest simulation models are increasingly capable of generating stable coexistence (Cheng et al. 2023; Cinoğlu et al. 2025) and could be combined with new methods to quantify coexistence mechanisms (Ellner et al. 2019, 2024). Regardless of approach, future coexistence research should prioritize rarely studied community types.

Similarly, we will not learn much about nature from MCT unless we quantify a wider variety of coexistence mechanisms. Most of the mechanistic partitioning studies we reviewed focused on temporal environmental variation, neglecting the many important coexistence mechanisms that do not depend on temporal fluctuations. This is not surprising given that MCT was initially designed to quantify fluctuation-dependent mechanisms whereas the more flexible, general approaches arrived recently (Ellner et al. 2019). Studies focused on fitness-density covariance in spatially variable environments should be a priority for future research. At broad spatial scales, the role of habitat heterogeneity in maintaining diversity is so obvious that quantifying it seems unnecessary: consider elevation gradients or sharp contrasts in soil type. At finer, within-community scales, however, describing relevant spatial environmental variation accurately enough for MCT applications is surprisingly difficult (but see Silvertown et al. 2015). We suspect that fitness-density covariance may be the strongest stabilizing mechanisms in many communities, but, to our knowledge, that intuition has yet to be tested. Ellner et al. (2024) developed new computational methods to quantify spatial mechanisms, but the need for empirical work is so great that even simple approaches dependent on crude assumptions would be welcome.

## 4.3 | Avoid Known Biases

Recent papers have highlighted a number of statistical problems that introduce bias in estimates of intra- and interspecific interaction strengths. Omitted variable bias occurs when a variable which affects both target individuals and their competitors is excluded from a statistical model and can bias estimates of competitive effects, in some cases even causing competitive interactions to appear mutualistic (Rinella et al. 2020). Regression dilution, which results from error in the measurement of competitor density, may cause overestimates of intraspecific competitive effects and underestimates of interspecific effects (Detto et al. 2019). The solution to both regression dilution and omitted variable bias is to use data from experiments where the density of competitors is precisely controlled and measured and/or to quantify measurement error. However, this is often impossible, especially for long-lived species where only observational data is available. In such cases, instrumental variable analysis (Rinella et al. 2020) and latent-variable modelling may help counteract data deficiencies (Detto et al. 2019). Finally, ignoring immigration into small census plots can cause intraspecific density dependence to appear stronger than it really is (Xu et al. 2023). As with omitted variable bias and regression dilution, this bias is more severe in observational studies. Avoiding, correcting or simply quantifying these biases by collecting better data, improving statistical models or validating model predictions with independent data (see Section 4.4) must be a priority for future MCT studies.

## 4.4 | A Plea for Validation

As discussed in Section 3, rigorous model validation is conspicuously absent from the typical MCT workflow, consistent with the culture of our discipline. Changing this culture will require a commitment to the expensive and time-consuming task of collecting truly independent data for model testing. First, we need to distinguish between model validation and model selection. Many MCT studies already address model selection by considering different functional forms to describe intra- and interspecific density-dependence. This is a critical step because the functional forms (e.g., Lotka-Volterra, Beverton-Holt) which best describe density dependence in any community are unknown and can determine the interpretation of processes such as higher order interactions (Kleinhesselink et al. 2022). The simplest solution is to compare the fit of several candidate models to data and select the best one (Terry and Armitage 2023). An alternative is to fit an ensemble of models, including a nonparametric alternative (e.g., Kristoffersen et al. 2001), and report results for each. Unfortunately, neither of these strategies answers the critical model validation question: how well does the model capture the true community dynamics? Given the different strengths and weaknesses of observational and experimental studies, we recommend different validation approaches.

Long-term observational studies have the strength of realism—they capture all the sources of variation in a system—but the weakness of poor control over potentially confounding variables. Mistaking causation for correlation may not result in poor predictions within the range of conditions captured in data used to train a model, but predictions based on extrapolations beyond those conditions will likely be poor. As a result, validation of models fit using observational studies should focus on testing the model, to the extent possible, under the novel biotic and abiotic circumstances considered in MCT counterfactuals. This recommendation goes beyond the traditional, minimal standard for model validation: can the model reproduce the data used in training? For example, Adler et al. (2010) reasoned that because their model did a reasonable job of capturing observed spatial patterns, individual size distributions, and year-to-year changes in plant cover, it could be relied on to simulate invasion growth rates under a range of scenarios. But this approach is weak because it does not test model predictions against independent data. A slightly higher standard would involve splitting the dataset into independent training and testing sets. However, even this kind of statistical validation does not address the problems discussed in the previous section: a model that skillfully predicts survival, growth, or short-term population growth under observed conditions may not make good predictions of long-term invasion growth rates under novel environmental conditions. A more rigorous validation test would use experimental perturbations to explore dynamics at boundary conditions. Perturbations of species densities via removals (Wootton 2001; Adler et al. 2018) or establishment of monocultures (Tuck et al. 2018) could test predictions based on the strength and direction of species interactions estimated from the training data. This kind of test is important because observational studies are especially prone to statistical biases in estimating the strength of density-dependence (Section 4.2). Perturbations of the environment (Adler et al. 2013), natural enemies, or symbionts (Chung and Rudgers 2016) could test the model's ability to predict the effects of other critical drivers of interest. Pairing a long-term observational study with an experiment is obviously more work, but it may be the only way to effectively build confidence in model-based conclusions about coexistence.

For experimental studies, the validation challenges are different. While carefully designed competition experiments avoid many of the biases that plague observational studies of competition, their weakness is a lack of realism. They are often conducted for short time periods, at small spatial scales, and typically feature only pairs of species or small subsets of a natural community, raising questions about how well they can predict dynamics of more species rich assemblages at larger spatial and temporal scales. In systems with faster generation times like microbial or *Drosophila* communities, model predictions can be tested with experiments (Terry 2025). For example, Hart et al. (2019) showed that predicted equilibrium abundances from a model fit to data from short-term competition experiments aligned well with the competitive outcomes observed in time-series. In a variation on this approach, Narwani et al. (2013) and Armitage and Jones (2020) tested predictions based on laboratory experiments with regional distribution data. For longer lived taxa, we could compare species equilibrium abundances predicted by a model fit to experimental data with the observed abundances at the time and place where the experiment was conducted. Pairwise experiments conducted for short periods may be unlikely to predict the high levels of species richness observed in natural communities (e.g., Kraft et al. 2015), but quantifying the difference is important because it indicates that the experiment likely excluded important coexistence mechanisms. Similar questions should be asked about experiments involving environmental manipulations: how realistically does the treatment mimic the environmental conditions? If long-term observational data are available, do species respond in consistent ways to the naturally-occurring environmental variation and the experimental treatment? On the other hand, for comparative studies of niche and fitness differences focused on mediators like plant–soil feedbacks, accurately predicting the outcome of competition in any specific community may be less important than capturing the contribution of the mediator to the invasion growth rate. In this case, or when a specific model form has been supported by previous system-specific studies, ensuring the external validity of the experimental results may be less important.

## 5 | The Future of MCT in Empirical Research

### 5.1 | Mechanistic Partitioning

We opened this paper by claiming that MCT has transformed coexistence research from a qualitative to a quantitative enterprise: instead of asking if mechanisms are operating or not, we can quantify them and compare their strengths. But our review of mechanistic partitioning studies resulted in mostly qualitative conclusions, reflecting the challenges of the mechanistic partitioning approach itself as well as the difficulties of comparing quantitative estimates of mechanism strengths across studies and systems. If nothing else, 20 years of empirical applications have given us a better understanding of the formidable challenges in partitioning coexistence mechanisms, especially in communities of long-lived organisms with complex life cycles. But these challenges are not a reason to abandon the goal of quantifying coexistence mechanisms. Even when we fall short of that goal, our efforts can advance ecology in unexpected ways. Development of new quantitative tools (Ellner et al. 2019) designed to make mechanistic partitioning studies easier to conduct can also serve conservation, such as plant community restoration (Aoyama et al. 2022). MCT concepts and tools have even been repurposed to study cancer (Miller et al. 2020) and disease dynamics (Cobey and Lipsitch 2012; Sieben et al. 2022; Park et al. 2024). MCT may be more likely to benefit society through the direct application of such tools than through the decades-long accumulation of general understanding about which coexistence mechanisms are most important in different ecosystems.

### 5.2 | Niche and Fitness Differences

Measuring niche and fitness differences under one set of conditions in one community offers limited information. As noted in Section 4.1, the real value of the niche and fitness difference approach is realized with comparisons of these metrics across experimental treatments or across species pairs to test general hypotheses about the biological processes that determine coexistence, and opportunities still exist to apply this approach to additional questions. For example, the question of how evolution shapes competitive outcomes is ripe for an MCT treatment. The process of character displacement aligns closely with the niche difference, while the evolution of competitive ability aligns well with the fitness difference (Yamamichi et al. 2022). MCT provides a theoretically justified approach to distinguish between these mechanisms using empirical data (Hart et al. 2019; Germain et al. 2020).

### 5.3 | In What Form Will MCT Persist?

Like all tools, MCT has limitations and will be improved and ultimately replaced. What features of MCT will be retained? The two defining features of MCT are its use of a quantitative measure of the stability of coexistence and its reliance on counterfactuals to partition contributions from different mechanisms. Whether the invasion growth rate is the best metric to partition is already an open discussion; alternatives such as time to extinction (Pande et al. 2020) or the sensitivity of an equilibrium (Barabás et al. 2012) could be substituted without altering the basic approach, or we could compare results for partitions of multiple metrics. However, we see no alternative to the reliance on counterfactuals. Understanding how a process influences coexistence requires comparison to community dynamics absent that process. Even the origin of coexistence theory, Gause's competitive exclusion principle (Gause 1932), is a counterfactual: in a world without niche differentiation, only one competitor could stably persist.

MCT's reliance on counterfactual comparisons is both its greatest strength and weakness. It is a strength because it is a powerful approach, fundamental to science in general. Every treatment in a randomized, controlled experiment represents a counterfactual and statistics for causal inference depend heavily on counterfactuals (e.g., Morgan and Winship 2014). At the same time, MCT's reliance on counterfactuals is a weakness because choosing counterfactuals is more art than science. In Chesson's original work (e.g., P. Chesson 1994), the use of small-variance approximations and 'standard parameters' produced a simple but very general partition of invasion growth rates, with counterfactuals—and thus coexistence mechanisms—corresponding to deletion of terms in the partition. The newer, simulation-based methods, while more general and flexible, do require explicit choices of counterfactuals (Ellner et al. 2019). Indeed, many of the theoretical critiques of MCT focus on problems of defining the counterfactual. With an infinite number of alternative realities to explore, how do we select just a few? For example, if we want to quantify the stabilizing effect of resource-use trade-offs, we could explore a world in which all species respond identically to every resource, or a world in which only one resource is limiting. Is one choice more appropriate? Our discomfort with this ambiguity is not a problem with MCT but with the open-ended nature of coexistence questions. MCT's lasting legacy may be our greater understanding of the precision needed to successfully frame and answer questions about coexistence mechanisms.

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### Author Contributions

All authors designed the study. P.B.A., Z.J.G., S.J.L., A.E.S., M.S., M.L.V. and J.M.L. conducted the literature review. P.B.A., M.D., S.P.E., T.L.G., J.I.L., J.M.L. and C.S. drafted portions of the manuscript, and all authors edited the manuscript.

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### Data Availability Statement

The data and code that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.ngf1vhj7c.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Studies included in our literature review. For 'Setting', 'lab' includes greenhouse and mesocosm experiments, while 'field' studies are conducted outdoors, without containers. Under 'Design', 'obs' refers to observational studies and 'exp' refers to experimental studies. Under 'MCT application', 'mediators' indicates that the study evaluated factors that influence the strength of niche and fitness differences or specific mechanisms. **Table S2:** The summary of the generalized linear mixed-effects model used to estimate the probability that temporal storage effects have a positive effect on invasion growth rates. **Table S3:** The summary of the generalized linear mixed-effects model used to estimate the probability that temporal relative nonlinearities in competition have a positive effect on invasion growth rates. **Table S4:** The summary of the generalized linear mixed-effects model used to estimate the probability that variation-independent mechanisms have a positive effect on invasion growth rates.