

# Moving beyond the “Diversity Paradox”: The Limitations of Competition-Based Frameworks in Understanding Species Diversity\*

Anita Simha,<sup>1,2,†</sup> Carlos J. Pardo-De la Hoz,<sup>1</sup> and Lauren N. Carley<sup>3</sup>

1. Department of Biology, Duke University, Durham, North Carolina 27708; 2. University Program in Ecology, Duke University, Durham, North Carolina 27708; 3. Department of Plant and Microbial Biology, University of Minnesota Twin Cities, St. Paul, Minnesota 55108

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**ABSTRACT:** Over the past century, ecologists have attempted to understand patterns of species diversity by showing stable coexistence arising from a baseline expectation of competitive exclusion. This expectation stems from an explicit assumption of resource scarcity and implicit assumptions of Malthusian struggle and winner-takes-all dynamics. Fidelity to the competitive exclusion principle (CEP) presents species diversity as a paradox: if species compete for limited resources, how can they coexist? In this article, we investigate the contradiction between the theoretical expectation of competitive exclusion and the empirical prevalence of multispecies communities. We trace the persistence of the CEP in ecological research despite numerous challenges and explore publishing trends suggesting that this framework has resulted in a disproportionate focus on competition and exclusion in contemporary research. From a critical science studies perspective, we analyze the sociopolitical factors that have contributed to these patterns. We argue that we must excavate the ideological foundation on which competition-based coexistence research has been built to move beyond the current perceived “diversity paradox.” To that end, we propose shifting the baseline expectation of coexistence research, introducing the notion of a coexistence principle, which positions the persistence of multispecies communities as the rule rather than the exception in nature.

**Keywords:** species coexistence, competitive exclusion principle, diversity paradox.

Facts are theory-laden, theories are value-laden, values are history-laden. (Donna Haraway 1991)

## Introduction

Contemporary ecological research employs a variety of approaches to study coexistence among species (Godwin et al. 2020). However, many of these stem from only a few historical precedents (McGehee and Armstrong 1977; Chesson 2000b; Barabás et al. 2018), focusing research over the past century predominantly on competition. Resultantly, a fundamental mismatch has arisen between the predicted prevalence of exclusion arising from competition and the observed levels of biodiversity in natural systems. One review of hypotheses about diversity maintenance succinctly summarized this perceived mismatch, positing that in light of the competitive exclusion principle (CEP), “the problem at hand is answering the question ‘Why do so many species coexist?’” (Palmer 1994, p. 511). Here, we argue that scientific frameworks structured by the assumptions of the CEP have caused the field to focus on mechanisms driving exclusion, therefore functionally asking why species do not coexist instead (Bertness and Callaway 1994; Gross 2008). While competition has clearly been shown to be an important process in ecological communities, the expected outcome of competitive exclusion cannot account for levels of diversity observed in nature. The CEP is analytically true (if any two species are identical in their ecological requirements, they cannot coexist), but we question the breadth of its utility to the ecological questions to which it is applied. By examining the political and economic contexts through which the CEP was produced, we trace its persistence in the

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† Corresponding author; email: [anita.simha@duke.edu](mailto:anita.simha@duke.edu).

**ORCID:** Simha, <https://orcid.org/0000-0002-8770-3029>; Pardo-De la Hoz, <https://orcid.org/0000-0002-7898-0948>; Carley, <https://orcid.org/0000-0003-1911-7025>.

face of counterevidence to its predictions and recommend future directions for research exploring species diversity.

### Origins of the Competitive Exclusion Principle

Competition-based frameworks—including the CEP, resource-ratio ( $R^*$ ) theory, and modern coexistence theory—have provided bases for much of the ecological research on species interactions over the past century (Armstrong and McGehee 1980; Tilman 1982; Chesson 2000a). In the 1930s, Gause developed a hypothesis of competitive dominance by conducting experiments with *Paramecium* and yeast species competing for food resources (Gause 1932, 1934a, 1934b). Using mathematical formulations from Lotka (1932) and Volterra (1926), Gause parameterized “coefficients of the struggle for existence” to model each species’ abundance as a function of its own and its competitor’s abundances (Gause 1932). Gause’s hypothesis, later popularized by Hardin as the CEP (Hardin 1960), states that if two species require the same ecological resources, the species better able to exploit those resources will outcompete the other. As such, this principle requires ecologists to find an explanatory axis of ecological differentiation to account for every instance of species coexistence.<sup>1</sup> Hardin justified the CEP with conventional wisdom in mainstream economics, in which individuals compete in an open market and seek to maximize utility in order to profit (Harvey 1974).<sup>2</sup> He further developed this idea by explaining that weaker competitors will naturally seek to favor themselves by restricting competition, which he contended was evident in the formation of labor unions by workers (Hardin 1960), naturalizing competition simultaneously in society and in nature (Muñoz-Rubio 2003).

Some decades later, MacArthur expanded the Lotka-Volterra approach used by Gause and modeled population abundances as functions of resource availability and species’ overlap in resource use (MacArthur 1972; Chesson 1990). This approach implies that the number of species persisting in a community should match the number of available resource axes (MacArthur 1972) or reflect specialization along a resource axis (MacArthur and Levins 1967). Tilman generalized this approach into the  $R^*$  rule, which states that if multiple species are competing for the same resource, then the one that can persist at lower levels of that resource will outcompete the other (Tilman 1980, 1982;

Chase and Leibold 2003). The  $R^*$  theory adapts micro-economic theory to explicitly model resource-use overlap between consumers (Rappart 1971; Covich 1972, 1974). Under this hypothesis, species coexist when they are competing for multiple resources and each is more limited by a different resource.

More recently, Chesson’s modern coexistence theory (MCT) has provided new tools to explore species coexistence (Chesson 2000a, 2000b; Barabás et al. 2018). In MCT, species persist when they can rebound from low abundances while competitors are at steady-state abundances (i.e., when each species has a population growth advantage over its competitors when rare). As such, mutual invasibility indicates that species may stably coexist. Equalizing and stabilizing mechanisms thus drive coexistence, with equalizing mechanisms reducing differences in species’ growth rates when rare and stabilizing mechanisms supporting species’ low-density growth rates (Chesson 2003); larger average fitness differences between species require greater niche differentiation to allow coexistence. All of these approaches adapted from Lotka-Volterra equations share assumptions that lead to the expectation of competitive exclusion for co-occurring species with similar ecologies.

### *Emergence of the Diversity Paradox*

Since the initial popularization of the CEP, its logical conclusion has been challenged by the ubiquity of coexisting species in nature (Hutchinson 1959, 1961; Valencia et al. 1994). Nevertheless, a common thread of competition-based frameworks is the assertion, either implicitly or explicitly, that it is difficult for species to coexist. Inconsistency between the theoretical expectations of competition-based frameworks and the empirical reality of multispecies communities—many of which are species rich (Wright 2002)—has created a supposed “diversity paradox.” Over the past 60 years, this paradox has motivated much community ecology research attempting to explain cases of coexistence as deviations from the expectation of competitive exclusion (Hutchinson 1961; Koch 1974; McGehee and Armstrong 1977). This paradigm is common in ecological thinking; when we surveyed the 100 most highly cited recent ecology articles on species diversity and coexistence (supplement 1), we found that 30 of them began with similar sentences that (1) frame diversity as an unsolved puzzle and (2) name understanding species coexistence as a main aim of the study. Data underlying this analysis are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.q573n5tjb>; Simha et al. 2022).

As evidence of the CEP’s function as a baseline expectation in community ecology, researchers must meet special criteria to falsify it: in Hardin’s articulation of Gause’s hypothesis, an axis of ecological differentiation between

1. “To assert the truth of the competitive exclusion principle is not to say that nature is and always must be, everywhere, ‘red in tooth and claw.’ Rather, it is to point out that every instance of apparent coexistence must be accounted for” (Hardin 1960, p. 1297).

2. “Any competitor knows that unrestrained competition will ultimately result in but one victor” (Hardin 1960, p. 1296).

species must be observed; in the  $R^*$  approach, a resource-use trade-off or sufficiently low resource-use overlap must be shown; and under MCT, a sufficient stabilizing and/or equalizing mechanism must be detected. All of these cases assume zero-sum benefit from the acquisition of a small number of scarce limiting resources, building a framework in which one species’ performance implicitly (in Lotka-Volterra models) or explicitly (in  $R^*$  models) comes at the expense of another’s. As such, the baseline expectation of any given species interaction is exclusion of an inferior competitor by the dominant one, unless a mechanism allowing their coexistence is detected.

Increasingly complex extensions of theory have emerged in an attempt to resolve the diversity paradox, but many updated approaches reinforce assumptions of the CEP (see “Contemporary Contexts” below).<sup>3</sup> These core assumptions may be ideologically informed, meaning that they justify a dominant worldview in society (Eagleton 1976). For example, the expectation in Lotka-Volterra competition models that the system of interest is spatially homogenous inherently constrains the range of parameter space in which coexistence is considered possible (Armstrong and McGehee 1980). Similarly, the assumption that ecological dynamics are governed by a small number of scarce resources, each unit of which can benefit only one or another competitor, necessarily results in a “struggle” for existence. Furthermore, logistical constraints to studying coexistence quickly become prohibitive in this framework; the focus on adversarial pairwise interactions generally precludes testing all of the possible interacting pairs in a natural community. As different ideologies may beget different biological assumptions to undergird theory, we argue that the assumptions leading to the CEP’s diversity paradox should be questioned (Rykiel 1996).

### *Contemporary Contexts*

Since the conception of this false paradox, many fruitful lines of inquiry have been stimulated to explain how species-rich communities seem to defy the CEP (Hutchinson 1961). For example, temporal variation in the performance of competitors has been documented as a mechanism promoting coexistence in stochastically varying environments (Chesson and Warner 1981). Beyond environmental heterogeneity, a suite of other processes and species’ attributes—including top-down controls (Estes and Palmisano 1974; Terborgh 2015), Janzen-Connell effects (Connell 1970; Janzen 1970), higher-order interactions and interac-

tion chains (Kerr et al. 2002; Allesina and Levine 2011; Levine et al. 2017), historical contingency (Fukami 2015; Fukami et al. 2016), intraspecific trait variation (Jung et al. 2010; Bolnick et al. 2011; Siefert et al. 2015; Uriarte and Menge 2018; Maynard et al. 2019), immigration (Loreau and Mouquet 1999; Esther et al. 2008), demographic heterogeneity (Gravel et al. 2011), and evolutionary dynamics (Pfennig and Pfennig 2012; Hart et al. 2019)—have all been explored as potential resolutions to the diversity paradox. While these lines of inquiry have provided rich contributions and new insights to our understanding of competitive species interactions, they explore the role of these factors within the underlying assumptions of the CEP. As such, hereafter we refer to such extensions as “refinements” to the CEP. Much recent work has explored CEP refinements (e.g., Narwani et al. 2013; Godoy and Levine 2014; Godoy et al. 2014; Kraft et al. 2015*b*; Germain et al. 2016; Letten et al. 2018; Matías et al. 2018; Petry et al. 2018; Grainger et al. 2019; Hallett et al. 2019), perhaps stimulated by the empirical tractability of MCT.

In addition to promoting refinements to theory, this body of work has revealed patterns in how ecologists study coexistence using the CEP. First, the broad adoption of MCT (presently) and its predecessors (historically) demonstrates that this framework, with its promise of identifying biological mechanisms underpinning coexistence, is appealing to many ecologists. Second, many contemporary studies on naturally co-occurring species conclude that the conditions for coexistence are restricted (Siepielski and McPeck 2010); indeed, when we surveyed a subset of contemporary coexistence studies (supplement 2), we found that most tested species pairs failed to meet criteria concluding stable coexistence (mean, median, and mode proportion of tested pairs concluded to coexist: 0.409, 0.375, 0). Data underlying this analysis are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.q573n5tjb>; Simha et al. 2022). This shows that when using CEP-informed approaches to measure species interactions, detecting stable coexistence is uncommon. Thus, studies exploring coexistence within a CEP framework may reveal that multispecies natural systems are infrequently at equilibria, as has been posited previously (Hutchinson 1961). The converse implication of this is that we appear to be adept at detecting competitive interactions when we test for them (Kraft et al. 2015*b*).

### *Limitations of Contemporary Approaches*

While admittedly not all research on species interactions aims to describe species-rich natural communities (e.g., see discussion of different applications of ecological models in Tredennick et al. 2021), many mechanism-focused studies are justified as relevant to this challenge. Nevertheless, the current body of work has not generated understanding

3. Here, we use “theory” to refer to “a hierarchical framework that contains clearly formulated postulates, based on a minimal set of assumptions, from which a set of predictions logically follows” (Marquet et al. 2014, p. 701), and we use “modeling” to refer specifically to mathematical approaches that apply the theory.

of how and why multispecies communities are generally the norm rather than the exception in nature. The failure of competition-based research to explain coexistence in natural communities may be driven by several methodological limitations that stem from key assumptions about competitive species interactions.

First, research in the CEP framework is, by definition, equipped to understand coexistence among competing species. Thus, clearly delimiting which species are and are not competitors becomes a central problem in coexistence research. In this vein, a core tenet of competition-based theories is that species are organized into guilds (*sensu* Simberloff and Dayan 1991) within which they must partition critical resource axes to coexist. However, our limited ability to understand and measure all axes of species' niches constrains our ability to determine whether co-occurring species are truly competing in the same guild (Gilbert et al. 1952).

Second, even assuming that species' assignments to competitive guilds are accurate, the limited dimensionality with which we can measure resource partitioning restricts the range of parameter space in which coexistence can be shown mathematically (Clark et al. 2010). Much research in the CEP framework was originally developed to understand communities of autotrophs and followed previous conceptions of niche dimensionality as relatively low, emphasizing key resource axes, such as light and moisture (e.g., Grubb 1977).

Third, multiple factors complicating the baseline expectations of the CEP (discussed above as "refinements") may act simultaneously. However, logistical feasibility constrains most empirical work to considering only one or a few of these at once.

Fourth, similar logistical constraints limit many studies to assessing interactions among a subset of species that co-occur in natural communities. The prevalent focus on pairwise interactions and the coefficients describing them is likely insufficient to describe ecological interactions in multispecies communities, in which the species present can themselves modulate the expression of these parameter values, generating nonadditive dynamics at the >2-species level (Saavedra et al. 2017; Muthukrishnan et al. 2020).

Beyond these methodological limitations, however, lies a more fundamental problem: the operationalization of the core concepts of the CEP requires experimenters to measure competition and then infer coexistence rather than measure or describe coexistence directly. Thus, while studies are framed as aiming to understand coexistence, they are in fact designed to test mechanisms of competitive exclusion. As previously mentioned, exploration of many refinements within this framework has yielded rich insight and useful advances. Furthermore, we acknowledge that falsification of and expansion from simple model assumptions is a com-

mon approach to scientific progress (Popper 1959). However, even generative exploration of refinements to the CEP does not overcome the fundamental limitations of competition-based frameworks, which frame competitive exclusion as the baseline model to be accepted until rejected (*sensu* Bausman 2018), place the onus of demonstrating the "possibility" of coexistence on the experimenter, and then constrain that possibility to a narrow window of parameter space. As a result, understanding coexistence remains an ecological holy grail precisely because we have rendered it so difficult to understand.

### Persistence of the False Paradox

#### *Entrenchment of the Competitive Exclusion Principle*

Despite the shortcomings explored above, much research on species coexistence remains guided by the CEP. As science is a socially embedded activity (Gould 1981; Haraway 1988), the CEP is reinforced by scientific norms, culture, and institutions. The assumptions that undergird the CEP—that resources are scarce, the environment is static, competitive interactions are the primary drivers of community dynamics, and success is zero-sum, among others—are ideologically informed and have been shaped by exchanges between the fields of ecology and mainstream capitalist economics over the past century. As examples, Lotka-Volterra population models have been applied to economic questions (Goodwin 1967), and  $R^*$  theory was influenced by mainstream microeconomics (Rapport 1971; Covich 1974; Tilman 1980).

While feedbacks between ecology and economics have been generative in some sense, they also reveal a shared underlying capitalist logic that is necessary to facilitate such interchanges. Indeed, Gause called Lotka-Volterra competition coefficients the coefficients of the "struggle for existence" (Gause 1934a), based on Darwin's usage of the phrase. In turn, Darwin was directly inspired by Malthus, a political economist who viewed human population growth as untenable owing to competition for limited food resources (Malthus 1798; Young 1969; Harvey 1974; Bowler 1976).<sup>4</sup> The premise that existence is inherently a winner-takes-all struggle becomes hidden in increasingly complex approaches to studying species interactions, but the Malthusian foundation of coexistence models remains in contemporary work.

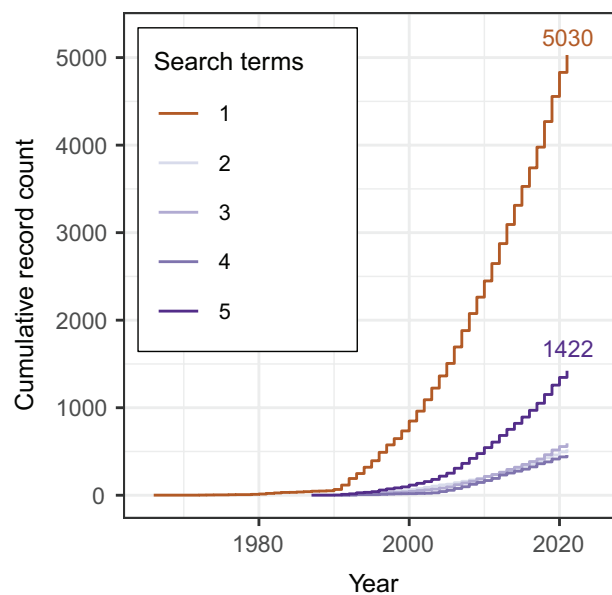
4. "I happened to read for amusement Malthus on *Population*, and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed" (Darwin 1958, pp. 42–43).



We are certainly not the first to identify these ideological roots of competition-based theories or to question their function. Indeed, the utility of the CEP as a grounding principle in ecological research has been the subject of recurring scientific debate (Cole 1960; Ayala 1969; Connor and Simberloff 1979; Gould 1988; Muñoz-Rubio 2003; Lewontin and Levins 2007). In response to Gause’s experimental work, early critics expressed skepticism about whether his conclusions drawn from laboratory studies of cultured microorganisms could be extrapolated to more complex field conditions (Gilbert et al. 1952), where assumptions such as environmental homogeneity may not be met. Later, Ayala (1969) provided experimental counterevidence to the CEP, showing that even when two competing species persisted at equilibrium, the mathematical conditions for stable coexistence were not met. This built on existing debate between those who saw the CEP as a useful expectation against which to structure experiments (Hardin 1960; Slobodkin 1961) and those who argued it was unhelpful or trivial (Andrewartha and Birch 1954; Cole 1960). Debate about the role of competition in structuring communities was particularly active in the 1970s and 1980s (Diamond 1975; Connor and Simberloff 1979; Connell 1983; Roughgarden 1983; May and Seger 1986), motivating an ongoing focus on manipulative experiments to elucidate that role. More recently, neutral theory has challenged a core assumption of CEP—that niche differences among species structure communities—instead positing that species can be ecologically equivalent (Hubbell 2001). Subsequently, neutral dynamics have been incorporated into competition-based frameworks (Adler et al. 2007).

Despite this diverse body of work critiquing competition-centric theory, the CEP became entrenched, framing competition as a natural expectation between species (Muñoz-Rubio 2003). Our analysis of the literature shows that while ecological research addressing “alternatives” such as neutral theory and positive interactions has increased over time, each of these topics has received an order of magnitude lower attention in the literature on coexistence than has competition (fig. 1). We posit that this pattern may be explained in part by ecologists studying interactions that they expect to shape communities rather than studying a diversity of species interactions “in relative proportion to their importance in nature itself” (Keddy 1990, p. 101) and that these expectations have been shaped in part by the political exchange described above.

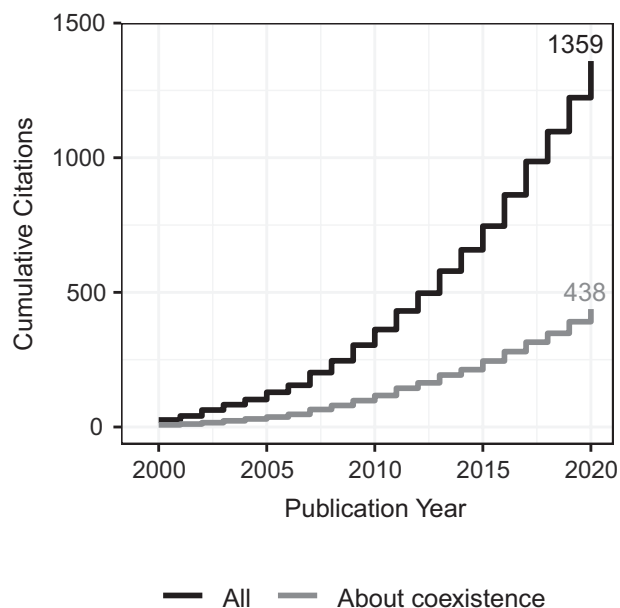
The intimate link between political economy and ecology is perhaps best evidenced in the work of Hardin; by consistently furthering right-wing eugenicist and nativist agendas through scientific outlets (Hardin 1960, 1971, 1974, 1994), his work provides a clear case study of how scientific understanding can be shaped by scientists’ politics. Paralleling the notion that monopoly is the natural result of unrestricted competition in economics, Hardin suggested that competi-



**Figure 1:** Cumulative number of ecology articles related to coexistence (1900 to present) and containing terms related to competition, mutualism and positive interactions, and neutral interactions. Search term 1: “coexist\* AND competit\*”; search term 2: “coexist\* AND mutual\*”; search term 3: “coexist\* AND positive interact\*”; search term 4: “coexist\* AND neutral\*”; search term 5: “coexist\* AND mutual\*” OR “coexist\* AND positive interact\*” OR “coexist\* AND neutral\*”. See supplement S3 for methods. Data underlying this figure are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.q573n5tjb>; Simha et al. 2022).

itive exclusion is the expected outcome of species interactions in ecological systems (Hardin 1960). In doing so, he naturalized the capitalist economic system to the point that the biological analog is true because of the economic one. This “double transference” occurs when biological phenomena are explained with social science claims, and the resulting framing of the biology is then used to justify the irrefutable truth of a social science claim (Foster and Clark 2008). The implication of this principle, framed through capitalist economics, is that any instance of species coexistence is aberrative from a naturalized expectation of competitive dominance and must be justified. As such, the onus of explaining coexistence when it is observed may be a consequence of capitalist ideology driving ecological thought rather than a necessary biological condition.

While Hardin’s political agendas are well-known and decades have passed since he articulated the CEP, his work has remained prevalent and continues to be frequently cited in ecological literature exploring conditions for coexistence (fig. 2). Several factors may contribute to the staying power of the CEP. The idea that the “most competitive” species should dominate may be intuitive to Western scientists precisely because it reflects the mainstream ideology reinforced



**Figure 2:** Cumulative count of articles citing Hardin’s 1960 article on the competitive exclusion principle between 2000 and 2020. The black line is the cumulative sum of all of the articles citing Hardin (1960), and the gray line shows the cumulative sum of articles that both cited Hardin (1960) and mentioned “coexist” (including “coexisting” and “coexistence”) in the article title or abstract. See supplement S4 for methods. Data underlying this figure are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.q573n5tjb>; Simha et al. 2022).

in capitalist societies (Eagleton 1976). Furthermore, ecologists have highly developed language to draw parallels between biological phenomena and market economics—including resource exploitation, scarcity, competitive dominance, and inferiority—but limited frames to consider alternatives. Even Clements’ “formations” of co-occurring species (Clements 1936), often considered to espouse interdependence, were based on competitive hierarchies (Kirchhoff 2020).

Though Hardin presumed literal parallels between ecological systems and capitalist economics that have been critiqued repeatedly by social scientists and humanists (Ostrom 1990; Hardt and Negri 2009; Harvey 2011), alternatives have not gained traction in ecology. Kropotkin’s conception of mutual aid, for example, explored the collective struggle of species in harsh environments (Kropotkin 1902). This influenced Wallace and early evolutionists and foreshadowed research on positive interactions but has received relatively little theoretical attention in Western scientific inquiry (Boucher 1985; Gould 1988; Dugatkin 2013; Smaldino et al. 2013; Lowrey 2015). Indeed, much more attention has been paid to competition and predation relative to mutualism in ecology education, as measured through textbook pages dedicated to each topic (fig. 3; Risch and

Boucher 1976; May and Seger 1986; Keddy 1990). Even current models of positive interactions employ capitalist logic, where resource exchange (read: market economy) among species modulates outcomes among interacting populations (Schwartz and Hoeksema 1998; Weyl et al. 2010; Holland and DeAngelis 2010; Johnson and Bronstein 2019; Johnson 2021; Valdovinos and Marsland 2021). This disproportionate emphasis on competitive interactions may bias ecological theory and experimentation (Bronstein 1994). Acknowledging and interrogating the ideological basis of scientific claims can improve scientific investigation and counteract such biases (Haraway 1988; Longino 1990; Harding 1992); however, such practices are not yet commonplace in mainstream ecology.

### *The Role of Scientific Institutions*

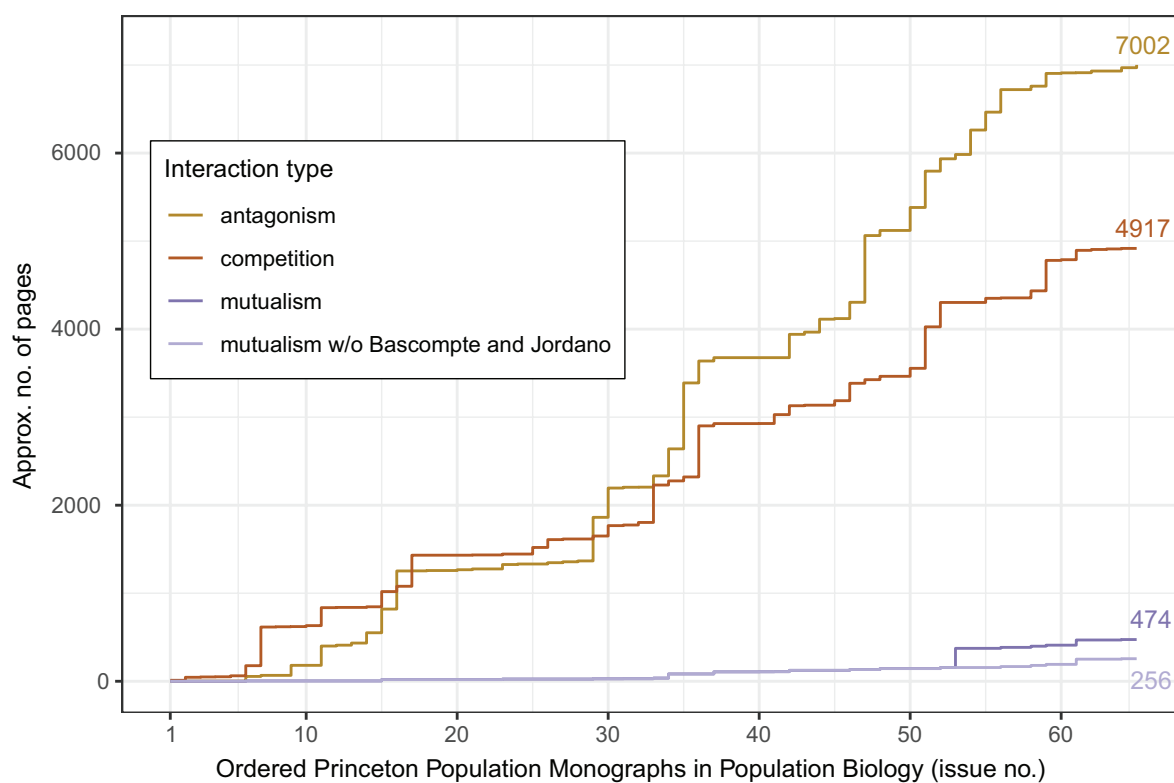
Because scientific norms influence what is perceived as acceptable, exciting, and fundable, researchers may perpetuate dominant frameworks like the CEP through their work even if they do not align themselves with the sociopolitical underpinnings of such frameworks; even as individual ecologists acknowledge the myriad mechanisms that can support species-rich communities, they must justify the tractability and impact of their research programs as they vie for funding resources (Levins and Lewontin 1985). Thus, scientific norms cause feedbacks that reinforce paradigms because (1) approaches with consensus support gain widespread usage and (2) widely used approaches gain consensus support (Latour 1999).

Furthermore, the structure of scientific institutions, time-limited research positions, and funding bodies can reinforce norms. The long-term effects of interannual environmental variation on coexistence, for example, may be difficult for a graduate student or postdoctoral associate with time-limited funding to sufficiently explore. When considering the persistence of the CEP, ecologists should recognize it as a powerful organizing principle against which research exploring observed coexistence and the diversity paradox can be pitted as baffling, novel, and worth funding. With resources supporting ecological research seen as increasingly scarce, efficient, high-impact research has become increasingly valued (Day et al. 2009). In this type of funding and publishing landscape, research programs undergirded by the CEP may be seen as safer intellectual investments with more scientific backing than alternatives.

### **New Directions for Coexistence Research**

#### *Expansions to the Current Paradigm*

The operationalization of models grounded in CEP assumptions frame resource competition as the primary



**Figure 3:** Cumulative number of pages in the Princeton Monographs in Population Biology series that mention mutualism compared with mentions of competition and enemy-victim interactions. Cumulative counts including and excluding Bascompte and Jordano’s (2014) monograph, which focuses on mutualistic networks, are distinguished. See supplement S5 for methods. Data underlying this figure are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.q573n5tjb>; Simha et al. 2022).

determinant of species coexistence. However, a variety of other patterns and processes have been shown to influence the ability of species to coexist (see “Contemporary Contexts” above). Empirical applications of MCT in the past decade have provided growing evidence for several such processes as coexistence mechanisms, but this approach reinforces the generality of the CEP: by framing the conditions of coexistence as system specific, idiosyncratic, or otherwise nongeneralizable, they are reinforced as deviations from the expectation of competitive exclusion. A study concluding that arrival order influences community assembly, for example, may be framed as a case study of historical contingency complicating the baseline expectation of competitive exclusion. We argue that within the current paradigm, further research into these refinements to the CEP is warranted to amass a weight of evidence and assess their generalizability. In some cases, patterns and processes that are currently seen as exceptions may in fact be the rule, although they have received comparably less research focus thus far (fig. 1).

Furthermore, while many studies grounded in competition-based frameworks aim to infer mechanisms allowing coexistence, some contemporary approaches to describing and predicting coexistence patterns creep beyond the bound-

aries of the CEP paradigm. For example, recent work using networks of spatial associations among species in assemblages across the world found that positive interactions among rare species may underlie their persistence in communities (Calatayud et al. 2020). In addition, some phenomenological models have shown excellent predictive power for describing patterns of diversity and coexistence outcomes in  $n$ -species pools (Clark 2010; Maynard et al. 2020). Toward the research goals of describing extant communities and/or predicting community responses to change, approaches seeking to infer coexistence mechanisms, such as mutual invasibility tests, may not necessarily be more useful than others, despite their biological appeal.

#### *A Principle of Coexistence*

The recommendations highlighted above illustrate some possible ways to expand our understanding of coexistence within a competition-dominated paradigm. In tandem with, and perhaps preceding, these efforts, we recommend moving beyond the diversity paradox by shifting community ecologists’ baseline expectation for species interactions. After all, asking the question how can species coexist itself

makes an assertion that coexistence is unlikely. We posit that instead, natural variation—including widespread coexistence, as evidenced by the prevalence of multispecies communities in nature—may often be the appropriate baseline expectation of ecological communities. Thus, we recommend that ecologists consider how a coexistence principle (CP) could restructure research on patterns of species interactions and biodiversity, starting with the assertion that given widespread variation in ecological communities and the environment, it is often unsurprising that many species persist in a particular area. As opposed to positioning the CP as a stand-in for the CEP with analogous questions, experimental designs, and models, we instead introduce it as a foundation for a new line of inquiry in which cases of coexistence do not require special justification.

An alternative framework like the CP could prompt ecologists to broaden both their perspectives about how questions are framed and the ways in which their research is conducted. Unsaddled by the tautological burden of demonstrating that diversity that already exists can (or should) exist, the range of questions that community ecologists might ask is vast. For example, rather than searching for mechanisms that allow coexistence to occur, we might instead focus on mechanisms that drive variation in diversity across space or time. Similarly, practitioners may choose to investigate “co-occurrence” with the same zeal with which they approach “stable coexistence,” given that stable coexistence appears rare in controlled experiments (see “Contemporary Contexts”) while co-occurrence is common. Mathematically “unstable coexistence” may still be ecologically important.

Through the lens of the CP, interpretation of some existing work as “explaining coexistence” may be reframed as evidence “explaining competitive exclusion” by falsifying the expectation of the CP (e.g., environmental homogeneity may be a mechanism supporting competitive exclusion). The CP can also lend framing to other well-studied biological processes besides competition that may limit coexistence, including dispersal limitation, environmental filtering, and evolutionary constraints (Felsenstein 1981; Levin 2000; Fraser et al. 2007; Kraft et al. 2015a; Cadotte and Tucker 2017; Hart et al. 2017), which CEP-undergirded frameworks do not consider.

Competition-based frameworks, including MCT, assume that potentially coexisting pools of species are ecologically similar and of the same guild and that their coexistence occurs at a scale at which population dynamics are not affected by dispersal (Chesson 2000a; Kraft et al. 2015a; Germain et al. 2020; Thompson et al. 2020). However, in natural communities, any given guild likely contains species that do not satisfy those assumptions about ecological similarity. Consideration of these processes besides competition that prevent species from coexisting within a CP framework could strengthen understanding of patterns of biological diversity.

We offer two recent suggested paradigmatic shifts in the field of evolutionary biology as relevant points of comparison to a proposed CP for ecology. In 2018, Kern and Hahn argued that current genomic data provide sufficient evidence to conclude that virtually no loci are free from the effects of natural selection, thus violating the premise of the neutral theory of molecular evolution. Like the CEP in ecology, neutral theory in evolutionary genetics has long served as a null hypothesis, or baseline expectation, against which to test “more interesting hypotheses” (Kern and Hahn 2018). However, the authors argue that a null hypothesis “overwhelmingly rejected” by data has, in this case, outlived its utility. While some of their claims have received pushback, these criticisms have not contested that the value of a null hypothesis not expected to hold true in biologically realistic scenarios is questionable (Jensen et al. 2019). In ecology, the ubiquity of multispecies communities despite abundant evidence of competitive interactions suggests that the CEP’s expected outcome of exclusion is likewise overwhelmingly falsifiable.

More recently, Monk et al. (2019) proposed that the assumption of a fitness cost to same-sex sexual behavior has stymied the understanding of variation in and evolution of diverse sexual behavior in animals. This example highlights the power of exploring proposed paradigm shifts through specific case studies; by focusing on a phenotype of interest (same-sex sexual behavior), Monk et al. (2019) not only critique the shortcomings of the baseline expectation in their case but also propose a concrete alternative model and recommend specific research directions to test it. Regarding the CEP in community ecology, we argue that robust case studies illustrating the shortcomings of the baseline already exist (see “refinements” above). As such, we frame this critique of the CEP and proposal of the CP in a general sense, as did Kern and Hahn (2018). Subsequent mathematical formalizations of such a shift in assumptions (Caswell 1988) could help structure future research in a CP framework.

While both proposed shifts in evolutionary biology were initially met with criticism (Jensen et al. 2019; Clive et al. 2020; Dickins and Rahman 2020), they have stimulated novel theoretical investigations (e.g., Johri et al. 2020; Lerch and Servedio 2021). We envision similar possibilities in community ecology. In such a future for the field, endeavors to characterize pairwise competition may still be useful but might best be restricted to questions and systems in which species diversity is already low or reduced.

Finally, we acknowledge that the alternatives discussed so far operate within mainstream Western science. Other epistemologies, including Indigenous, Black, and queer ways of knowing, have well-developed, long-standing lines of inquiry on the natural world that have been largely marginalized in academic ecology, despite exemplifying viable



alternatives to it. For example, Indigenous frameworks, such as kincentric ecology, ecological balance, and services to ecosystems (Salmón 2000; Comberti et al. 2015; Reo and Ogden 2018), have improved management goals like fire stewardship and conservation (Fraser et al. 2006; Marks-Block et al. 2019; Hart-Fredeluces et al. 2021). We advocate for engagement with and legitimization of a diverse set of knowledge systems by scientists but also stress that those doing so should take care to utilize methodologies that do not reproduce extractive and colonial relationships (Smith 1999; Tuck and Yang 2012; Liboiron 2021).

### Conclusions

We hope that research based on a CP might broaden the scope of questions that ecologists ask about species interactions and shift the current baseline of expected outcomes in coexistence research. We also hope that this perspective will increase critical reflection on the ways that social contexts and institutional limitations influence the formation and entrenchment of scientific paradigms.

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### Statement of Authorship

All authors contributed to the conceptualization, literature review, data analysis, data visualization, and writing of the manuscript.

### Data and Code Availability

All data used in analyses and code for generating figures are publicly available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.q573n5tjb>; Simha et al. 2022).

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