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Facilitation Thinking for Coexistence Theory

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ABSTRACT

Species interactions are foundational to biodiversity maintenance. Facilitation, a common outcome of species interactions, occurs among and between a wide variety of organisms yet its treatment in the theory and models used to predict species coexistence is underdeveloped. We ask why this is and speculate about how to address this apparent discrepancy. We first evaluate a persistent ambivalence to facilitation in the context of population and community ecology, particularly in contemporary coexistence theory. We then propose 'facilitation thinking' to remedy the gap between empirical evidence of facilitation and mathematical theory of coexistence. We briefly discuss how a holistic treatment of facilitation in theory has the potential to reconfigure our basic understanding and definition of coexistence. Ultimately, we argue for an expanded theory of coexistence that accounts for a diversity of species interaction outcomes, allowing for the study of interactions and diversity maintenance beyond the war of all against all.

[A]ttempts to breach the acceptable are summarily dealt with, occasionally by devastating criticism, but far more frequently by neglect and ignorance

—Margulis and Sagan (1997)

1 | Problem Statement

A central goal of ecological theory is to explain and predict patterns observed in nature. Coexistence theory generally relies on the premise that competition drives coexistence, and that facilitation is either irrelevant, uncommon, or detrimental to coexistence. However, facilitative interactions are common in nature. Given the universality of both facilitative interactions and diverse, coexisting communities of organisms, we argue that we lack theory that can properly account for and explain how facilitation drives coexistence dynamics. This paper calls for the iterative development of such theory, with the goal of improving our explanations and predictions of community diversity.

2 | Facilitation and Coexistence Theory Are at Odds

Facilitation is an interaction outcome whereby an individual or population performs better in the presence, or increased density of, an interaction partner(s), than when that partner is absent or at lower densities (Levin 2012; Bertness et al. 2024). Facilitation can occur within (intraspecific) or between (interspecific) species, and across or within trophic levels, but is most often used to describe interactions within trophic levels and among sessile organisms, especially plants. Evidence of intra- and interspecific facilitation in natural systems is common, with little evidence that these interactions are particularly weak or rare (e.g., Bertness and Callaway 1994; Callaway 1995, 2007; Goldberg et al. 1999; Brooker et al. 2008; McIntire and Fajardo 2014; Bertness et al. 2024).

Coexistence theory attempts to explain and predict if and how species can persist together in biological communities. This body of theory has developed over the last 60 years, motivated by the well-known Hutchinsonian paradox: how can co-occurring populations of species competing for the same resources stably persist? (Hutchinson 1961) As Simha et al. (2022) explain, embedded in this question is the basic assumption that competition drives coexistence—that is, we begin by asking *how* competition maintains coexistence, rather than *whether* it does. Indeed, in current theory, coexistence is framed as possible when intraspecific (within-species) competition balances interspecific (between species) competition such that competing species can grow from low densities in each other's presence.

The competitive worldview exemplified by Hutchinson's paradox pervades contemporary ecology. At its core, this worldview presupposes the existence of individual, autonomous units whose most important interaction is battling with each other to secure limited resources (Lotka 1920; Volterra 1926; Gleason 1926; Gause 1934; Hardin 1960; Whittaker 1965). Discussions of the limitations of this worldview—what we call 'competition thinking'—for the progress of theory are not new, nor are they restricted to the fringes of ecology (Cole 1960; Bronstein 2009; McIntire and Fajardo 2014; Wright et al. 2021; Simha et al. 2022). However, change in how coexistence specifically is conceptualised and mathematically modelled has been slow to progress. We suggest that this is not due to some inherent mathematical challenge, but because we overestimate the importance of competition and underestimate the importance of other kinds of species interaction, that is, facilitation, for coexistence. We explain below.

The attachment to competition thinking has emerged in part due to the premium placed on mathematical models as predictive and explanatory instruments in coexistence research. Classical mathematical models of coexistence (from which facilitation is conspicuously absent) constitute the bedrock of community and population ecology (e.g., Lotka 1920; Volterra 1926; Ricker 1952; Beverton and Holt 1957; Tilman 1982). The vast majority of population models in use today are still based on these models, which are rooted in the principle of resource competition: individuals compete for scarce and/or limited resources, and this competition affects population growth rates. In this version of coexistence, inter- and intraspecific facilitation disrupt coexistence by promoting unbounded population growth and threatening equilibrium (May 1981).

With this framing, modelling competition as the only important interaction outcome for coexistence seems logical and mathematically robust. However, the 'first principle' of competition stands in stark contradiction with the considerable and ever-mounting evidence that facilitation is also common and widespread across many ecosystems (e.g., Neiring et al. 1963; Shmida and Whittaker 1981; Callaway 1995; Roll et al. 1997; Bruno and Bertness 2001; Chu et al. 2008; Bakker et al. 2013; Soliveres et al. 2015; Gross et al. 2015; Leverett 2017; Maestre et al. 2017; Bimler et al. 2018; Kinlock 2019; Bergamo, Streher, Traveset, et al. 2020; Bergamo, Streher, Wolowski, et al. 2020; Picoche and Barraquand 2020; Molinari et al. 2022; Wang et al. 2022; James et al. 2023; Bertness et al. 2024; Bimler et al. 2024; Buche et al. 2024). For example, facilitation accounted for 38% of over 10,000 reported plant interactions in a recent meta-analysis (Yang et al. 2022).

When coexistence is necessarily defined as a function of competition and stable equilibria, facilitation and disequilibrium are theoretically lashed together, and jointly confer a lower probability of coexistence (e.g., Spaak and Schreiber 2023). The empirical evidence for this theoretical framing of facilitation can be interpreted to mean one of three things: (1) while widespread, the effect of facilitation is almost always so low as to be effectively meaningless for coexistence; (2) because facilitation is widespread, many communities of plants are under constant threat of disequilibrium and have few pathways to stable coexistence; or (3) the analytical tools which have emerged from the competition thinking tradition are ill-suited to investigate the role of facilitation in coexistence.

Until recently, mathematical theory has mostly developed under option (1), where facilitative interactions are either regarded as exceptional or inconsequential. As a result, facilitation in coexistence is typically either ignored, studied under distinct and separate frameworks (mutualisms, e.g., Thébault and Fontaine 2010; Rohr et al. 2014; Gracia-Lázaro et al. 2018), or relegated to case studies of isolated importance such as extremes of abiotic stress (stress gradient hypothesis, e.g., Bertness and Callaway 1994; Soliveres et al. 2015), singular moments in life history (plant recruitment networks, e.g., Verdú and Valiente-Banuet 2008) or community succession (priority effects, ecosystem engineering, e.g., Ke and Letten 2018). This fragmentation of the research (see Data S1.1 for a list of the many terms describing facilitation) makes it difficult to envisage any unifying principles governing the role of facilitation in diversity maintenance.

In response to broad calls to integrate facilitation into ecological theory (Bruno et al. 2003; McIntire and Fajardo 2014; Soliveres et al. 2015; Michalet and Pugnaire 2016), theoretical advances allow us to quantify how facilitation affects competitive coexistence when certain assumptions are met (Table 1). The picture painted by this work generally aligns with option (2). For example, Spaak and De Laender (2020) and Spaak and Schreiber et al. (2023) show how facilitation confers a destabilising effect on coexistence, implying (though not explicitly acknowledged by the authors) that if facilitation is widespread, then stable coexistence must commonly be under threat. While we acknowledge that facilitation need not have a purely positive effect on coexistence and diversity (e.g., Bulleri et al. 2016), these studies tend to build upon the competitive population models described above. A close examination of the underlying assumptions reveals that competition thinking still dominates: facilitation is modelled as a reduction in competition (Ke and Letten 2018; Schreiber et al. 2019; Johnson et al. 2022); or is allowed but with the caveat that the net effect of interactions must still be competitive (Ellner et al. 2019); or weak interspecific facilitation can occur, but intraspecific facilitation cannot (Spaak and De Laender 2020; Spaak and Schreiber 2023); or the presence of facilitation means coexistence cannot be predicted (Majer et al. 2024). While we celebrate the advancement these models represent, they also illustrate how competition thinking implies a certain precariousness of coexistence in the face of facilitation, that seems out of keeping with natural observations. Thus we ask, could this really always be true?

Given that facilitation and communities of apparently stably co-existing plants are both widespread, we are curious about the potential for models that take option (3) seriously: what if our theory is insufficient, and facilitation is a key driver and potential promoter of coexistence? Using models based in competition thinking may impede the development of theory that can answer this question. We propose 'facilitation thinking' as a way to reposition thought to address this blind spot in coexistence theory. Importantly, facilitation thinking does not preclude the existence or importance of competition in nature—we wholeheartedly agree that competition is important. Rather, it assumes that important coexistence dynamics can also commonly result from the positive effects of organisms on each other, separately from competition.

TABLE 1 | Recent models of diversity maintenance that allow for facilitation.

References	Coexistence framework	How is facilitation addressed?	Empirical case study?	Hurdles for facilitation thinking
Ellner et al. (2019)	Modern coexistence theory	Quantifies contribution of facilitative interactions to invader growth rates and coexistence	Yes	Net effect of interactions must be competitive, intraspecific interactions must be competitive
Koffel et al. (2021)	Niche theory	Expands classical niche concepts to include facilitation	No	Niche models are complex and difficult to parameterize with empirical data; proposed niche metrics are limited to two-species cases
Spaak and De Laender (2020)	Modern coexistence theory	Redefines niche and fitness differences to allow for interspecific facilitation	Yes	Intraspecific interactions must be competitive
Spaak and Schreiber (2023)	Modern coexistence theory	Predicts multispecies coexistence, interactions can be facilitative	Yes	Intraspecific facilitation destabilises coexistence

3 | Qualities of Facilitation Thinking

What does a theory of facilitative coexistence look like? To head off any suspense: we don't quite know yet, and there are many possible answers. However, there is no biological evidence to suggest that positive interdependence is not a viable mechanism for maintaining diversity (Valiente-Banuet and Verdú 2010; Butterfield et al. 2013; McIntire and Fajardo 2014). The value judgement we make when developing theory under the auspices of competition thinking is that maintaining competition as the primary driver of coexistence is more important than seriously considering facilitation as a different but equally viable driver. This constrains not only mathematical models and definitions of coexistence, but also empirical studies and the interpretation of their results. For example, empirical estimates of facilitation are regularly discarded (e.g., Narwani et al. 2013) or fixed to zero (e.g., Levine and HilleRisLambers 2009; Godoy et al. 2014; Wainwright et al. 2018; Bowler et al. 2022; Van Dyke et al. 2022) during analysis because they cannot be used to make predictions of coexistence in existing frameworks. The desire to link mathematical theory with natural observations and empirical work (e.g., Grainger et al. 2019; Godwin et al. 2020) can thus inadvertently retrench competition thinking in coexistence research (Bertness and Callaway 1994; Bertness and Leonard 1997). Using facilitation thinking as theoretical context requires that we examine and minimise competition bias in experimental design, the treatment and transformation of raw data, and population models and quantitative tools we use to analyse and interpret data.

A crucial assumption of facilitation thinking is that facilitation does not reduce to competition but can act to promote coexistence in a distinct way. Facilitative coexistence must then be based on models that incorporate the contributions of facilitation to population dynamics beyond the weakening of competition. Even in cases where the 'net effect' of one species on another is competitive, this means disentangling the product of relative intensities of different interactions (Hunter and Aarssen 1988;

Callaway et al. 1991). Building 'unreduced' facilitation models necessitates a deeper understanding of the drivers of facilitation (as discussed by Bronstein 2009) which can be supported by empirical investigations free of competition bias.

Like competition, facilitation is likely not randomly distributed through time and space. When and under which circumstances facilitation occurs will have important consequences for the kind of theory that develops out of facilitation thinking. The decisions we make when quantifying interaction outcomes (e.g., choice of proxy or data manipulation, see Freckleton and Watkinson 2000) are all informed by theoretical norms (Layman and Rypel 2023), creating opportunity for competition bias. For example, predicting when and where facilitation occurs has been investigated primarily through the lens of the stress gradient hypothesis (SGH), which predicts that facilitation increases with abiotic stress (Bertness and Callaway 1994). Empirical evidence bears the SGH out in plants (reviewed extensively in Austin et al. 2004; Maestre et al. 2005; Padilla and Pugnaire 2006; He et al. 2013; Piccardi et al. 2019). However, the strength of this hypothesis and its evidence has led to some amount of neglect in searching for facilitation in systems that are not stressful, contributing to a potentially conservative understanding of where and when facilitation occurs (McIntire and Fajardo 2014).

4 | Three Steps Towards Facilitation Thinking for Coexistence Research

Integrating facilitation into an updated theory of coexistence raises both practical and philosophical considerations. We are doubtful that any coexistence framework based in competition can be used to holistically understand the role of facilitation in coexistence. How then do we develop new theoretical constructs? We suggest three tangible steps to make the transition. In new studies of species interactions, researchers should: (1) measure species interactions without bias to understand the true prevalence of facilitation, (2) build models that can translate a wide range of interaction outcomes into population performance, and (3) experiment with redefining coexistence.

Gaining a better grasp of the commonality and strength of facilitative interactions is necessary to understand when and where facilitation is important to coexistence. To combat the creep of bias into how we estimate species interactions, we suggest a strong investment into 'quantitative natural history', or the quantification of observations without preconceived expectations of what details are and are not important. Much can be gained on this front by statistically reanalysing existing data using methods that do not assume the shape, direction, and magnitude of interaction outcomes—for example, using generalised additive models (GAMs, Wood 2017).

Mathematical modelling work to include facilitation in coexistence theory and predictions is ongoing. A small but promising body of research has shown that facilitation is important for population dynamics or mutual persistence when variation along some axis is accounted for, rather than ignored or averaged out (e.g., differences in growth stage, see Martorell and Freckleton 2014). Accounting for variation may thus be crucial to detecting facilitation and its effects on coexistence. Therefore, to build on and expand existing modelling efforts, we will need more complex (less reductive) models of how species interactions affect performance, and how this affects population dynamics (Stouffer 2022). This can be guided by empirical evidence that links variation in time or space to facilitation. Exploratory work can be done by building one or more sources of variation into models of coexistence; we recommend adapting and expanding existing modelling approaches (Table 2). In these efforts, the key is to incorporate facilitation such that its effects are attenuated in some way that prevents runaway population growth (Callaway and Walker 1997; Callaway 2007; Hart 2023). This is not a new idea and has been explored previously in models of mutualisms (Holland and DeAngelis 2010; Hale and Valdovinos 2021), single-population models (e.g., intraspecific facilitation in the form of Allee effects; Stephens et al. 1999) and resource-explicit models (Koffel et al. 2021). We break these ideas into six broad categories of ecological variation: location or time, life history stages, trophic interactions, scale, population density, or higher-order interactions (see Table 2 for details).

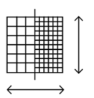
Finally, facilitation thinking may require that we re-evaluate how we define and quantify coexistence. Most formal definitions rely on strict mathematical criteria (Grainger et al. 2019; Johnson and Hastings 2022; Clark et al. 2024) and analytical investigation, which favours the study of competitive low-diversity systems with stable equilibria. Computational advances may mean we are no longer restricted to that approach. One promising way to redefine coexistence is to define it probabilistically, where species can be said to coexist to a degree (this is already happening in competition-based coexistence modelling, e.g., Bowler et al. 2022). Another option is to treat it as unquantifiable at the scale of pairwise interactions and instead only evaluate coexistence as an emergent property at the scale of multi-species assemblages (as seen in competitive intransitivity networks, e.g., Laird et al. 2006, and species interaction networks, e.g., Bimler et al. 2024). Simulations may allow us to evaluate if species maintain positive abundances as a community in the presence of facilitation. A benefit of this approach would be the ability to analyse coexistence over shorter, more relevant timescales, rather than over theoretically infinite time (e.g., Schreiber et al. 2023; Vollert et al. 2024).

5 | Conclusion

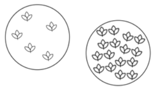
If facilitation and coexistence are both as common and widespread in natural systems as empirical evidence suggests, then our current understanding of coexistence is at least incomplete. Philosophically, the idea of facilitative coexistence offers an opportunity to engage with alternative constructions of how life is organised. Facilitation thinking may lead to completely different ways to imagine coexistence: how would we model coexistence as a common, robust phenomenon arising from interdependent, mutable, and fluctuating entities engaged in simultaneously facilitative and competitive interactions?

The steps we propose for developing coexistence theory with facilitation thinking may seem unsatisfying because they do not provide a single, clear solution. What we aim to address, however, is the narrow frame-of-mind that is the default in

TABLE 2 | Approaches for incorporating variation into existing coexistence models.

Axis of variation	Potential modelling approaches	Example references
Location or Time 	Borrow from source-sink dynamic and metacommunity ecological theory. In these models, population(s) are distributed on a landscape that varies either discretely or continuously across space. Extending these types of models to include species interactions that are positive in some locations and negative in others (e.g., due to variable stressful conditions as in the SGH) would clarify how facilitation might affect population regulation and community structure, which when considered with dispersal might determine if and how subpopulations rescue each other by spreading success across subpopulations distributed through space.	Shmida and Ellner (1984); Holt (1985); Pulliam (1988); Danielson (1991); Leibold et al. (2004); Martorell and Freckleton (2014); Stouffer et al. (2018)
Life-history stages 	Stage-structured models could allow for the effects of facilitation in one life stage to interact with, and potentially be attenuated by, the effects of competition in another life stage to determine overall fecundity or performance. Several simulation studies have shown that, theoretically, such dynamics can foster annual plant coexistence. Stage-structured models of interactions that borrow from the literature on ontogenetic niche shifts (typically studied in fish, amphibians, and other animals that go through metamorphosis) may be a path forward.	Gross (2008); Nakazawa (2015); Aubier (2020); Kinlock (2021)
Trophic interactions 	Shared mutualists or antagonists have already been incorporated into some models of coexistence. These models have limited ability to interrogate how facilitation affects coexistence because they constrain pairwise species interactions to be competitive. This approach to modelling species interactions can, however, still be useful for investigating how the positive effects of sharing mutualists (e.g., joint attraction/recruitment) can discount the negative effects of competition for resources, but may need to be combined with other approaches to explore its potential for studying facilitation. Network models of interaction modules may provide a path forward, and have been used to investigate how coexistence is stabilised via apparent facilitation, where two species benefit each other via a shared mutualist.	MCT and structural coexistence approach: Kuang and Chesson (2009); Kuang and Chesson (2010); Bartomeus et al. (2021); Johnson et al. (2022); Network approach: Sauve et al. (2016); Losapio et al. (2021)
Scale (space/ time) 	Long-distance facilitation and long-term facilitation have been modelled using Lotka-Volterra models of competing populations, by allowing for facilitation to occur via amelioration of patch conditions at a distance (space), or through supporting a shared mutualist through time. Each approach is limited in its ability to incorporate facilitation into interaction coefficients of the Lotka-Volterra model, but allows for facilitation to occur indirectly at a larger spatial scale or a longer time scale.	Wang et al. (2022); James (2023)

(Continues)

Axis of variation		Potential modelling approaches	Example references
Population density		Nonlinear responses to increasing neighbour densities is relatively well-explored in the context of the Allee effect, where increasing conspecific density confers a benefit for individuals or population growth rates at low densities (a facilitative effect), but becomes detrimental or less beneficial at high densities. This principle could be applied to models featuring nonlinear patterns in vital rate or population growth rates in mixed-species communities.	Goldberg and Werner (1983); Dickie et al. (2005); Chu et al. (2008); Stephens et al. (1999); Berec et al. (2007); Kramer et al. (2009); Livadiotis and Elaydi (2012)
Higher-Order Interactions		The inclusion of facilitation via higher-order interactions into coexistence models expands opportunities to detect coexistence through a wider range of mechanisms than are possible in traditional MCT models. This approach needs development because HOIs present a number of computational challenges that have yet to be fully resolved. These models are likely to become more useful when combined with metapopulation metacommunity, or network models that are better suited to high levels of complexity.	Mayfield and Stouffer (2017); Stouffer et al. (2018); Singh and Baruah (2019); Li et al. (2021); Martyn et al. (2021); Majer et al. (2024)

coexistence research. This is not resolvable in one paper, as there are many possibilities for how to incorporate facilitation into coexistence depending on the approach (empirical, statistical, simulation-based, and/or analytical). Long-term, substantial changes in theory will likely only eventuate after a period of exploration and concerted expansion of thought beyond existing theory. We thus encourage readers to engage in facilitation thinking as a way to create novel concepts, methods, and tools to expand and refine our understanding of the ecological processes driving the maintenance of diversity.

If facilitation thinking becomes common, we predict wide-reaching benefits for understanding ecological phenomena. Given that competitive coexistence theory is reaching its limits of prediction and explanation (Chang et al. 2023; Spaak and Schreiber 2023; Bimler et al. 2024), facilitation thinking offers a way to expand and improve how we quantify and interpret the patterns we observe in nature.

Author Contributions

A.R.M.J., M.D.B. and M.M.M. jointly conceived of, designed and wrote this viewpoint. A.R.M.J. was assigned first author and M.D.B. assigned last and corresponding author to reflect equal lead contributions.

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The authors declare no conflicts of interest.

Data Availability Statement

The authors have nothing to report.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.