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Functional coexistence theory: Identifying mechanisms linking biodiversity and ecosystem function

Joe Wan[1,2] | **Po-Ju Ke**[1] | **Iris Hordijk**[2,3] | **Lalasia Bialic-Murphy**[2] | **Thomas W. Crowther**[2]

[1]Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan

[2]Department of Environmental Systems Science, Institute of Integrative Biology, ETH Zürich, Zürich, Switzerland

[3]Forest Ecology and Forest Management Group, Wageningen University & Research, Wageningen, Netherlands

Correspondence
Po-Ju Ke
Email: pojuke@ntu.edu.tw

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Abstract

Theory and experiments show that diverse ecosystems often have higher levels of function (for instance, biomass production), yet it remains challenging to identify the biological mechanisms responsible. We synthesize developments in coexistence theory into a general theoretical framework linking community coexistence to ecosystem function. Our framework, which we term functional coexistence theory, identifies three components determining the total function of a community of coexisting species. The first component directly corresponds to the niche differences that enable pairwise species coexistence and to the complementarity component from the additive partition of biodiversity effects. The second component measures whether higher functioning species also have higher fitness under competition, providing a missing link between the additive partition's selection effect and modern coexistence theory's concept of equalization. The third component is least well studied: reducing functional imbalances between species increases niche difference's positive effect on function. Using a mechanistic model of resource competition, we show that our framework can link the structure and function of multispecies communities and that it can predict changes in coexistence and ecosystem function along gradients of resource availability. In particular, we expect the effect of resource level on biodiversity–function relationships to be limited in magnitude and variable in sign because it should be primarily mediated by fitness. Next, we confirm our theoretical expectations by fitting this model to data from a classic plant competition experiment. Finally, we apply our framework to simulations of multiple ecosystem functions, demonstrating that relationships between niche, fitness, and function also predict a community's multifunctionality, or ability to simultaneously show high levels of multiple functions. Taken together, our results highlight fundamental links between species coexistence and its consequences for ecosystem function, providing an avenue toward mechanistic and predictive understanding of community–ecosystem feedbacks.

KEYWORDS
coexistence, complementarity, fitness difference, mechanistic model, multifunctionality, niche difference, selection, transgressive overyielding

INTRODUCTION

All living systems obey the same set of physical laws, yet any individual ecosystem encompasses a unique assembly of organisms and interactions. This fundamental contrast is embodied by a traditional division within ecology: ecosystem ecology focuses on the flow of energy and nutrients as common currencies, while community ecology aims to explain the diversity of organisms. However, understanding ecosystems requires ecologists to acknowledge the fundamental links between these aspects: ecosystem flows affect community composition; in turn, ecological communities control ecosystem cycles of energy and nutrients. Thus, general theories of ecosystems must account for the feedback between ecosystem and community processes. As human activity simultaneously perturbs global element cycles and threatens local biodiversity, understanding such feedback is a fundamental ecological challenge with enormous practical consequences for understanding and mitigating global change.

One successful body of research, termed *biodiversity–ecosystem function*, studies this feedback by asking how diversity at the community level affects function at the ecosystem level (e.g., biomass production, nutrient cycling, or ecosystem services). This field has combined manipulative experiments (Hector et al., 2002; Hooper et al., 2005) and theoretical analyses (Loreau, 2004; Turnbull et al., 2013) to highlight the effect of biodiversity on ecosystem processes (Hector et al., 2002; Isbell et al., 2017). The effect of biodiversity on ecosystem function can be partitioned into two components: *complementarity*, which measures whether species function better on average within communities versus growing alone (e.g., due to underlying niche differentiation), and *selection*, which measures whether higher- or lower functioning species disproportionately dominate a community (Loreau & Hector, 2001). This approach, termed the *additive partition* of biodiversity effects, and subsequent related frameworks (Bannar-Martin et al., 2018; Clark, Barry, et al., 2019; Fox, 2005; Isbell et al., 2018) have been applied to a variety of experiments and empirical studies. Taking advantage of this theoretical–empirical synthesis, a cross-scale perspective has emerged (Cardinale et al., 2009; Hooper et al., 2012; O'Connor et al., 2017), emphasizing the positive effects that biodiversity often has on ecosystem function.

Nonetheless, the degree to which biodiversity promotes ecosystem functioning (i.e., a positive diversity–function relationship) varies greatly between systems (O'Connor et al., 2017). While most work has focused on biomass production in terrestrial plants, the positive diversity–function relationships observed there may not generalize across ecosystem types (O'Connor et al., 2017) with different species pools, environmental conditions (Spaak et al., 2017), or community structures (Hordijk et al., 2023). Indeed, in certain highly competitive systems, consistently negative diversity–function relationships may be the norm (Maynard et al., 2017). Furthermore, even within systems, diversity–function relationships vary during community succession (Weis et al., 2007), suggesting that the observed positive effects of biodiversity may sometimes be transient (Turnbull et al., 2013). Accordingly, though recent empirical (Gonzalez et al., 2020; Liang et al., 2016) and modeling work (Pavlick et al., 2013) has begun to focus on applying the insights of diversity–function studies at large scales, synthesizing a general predictive theory of ecosystem function remains challenging. Thus, an important current challenge for understanding and predicting community–ecosystem feedbacks is identifying the underlying ecological mechanisms—that is, interactions between species and their environment—through which diversity affects function (Hector et al., 2009; Loreau, 2010; Loreau et al., 2012; Mouquet et al., 2002).

Just as the additive partition has provided a unifying tool for linking diversity to ecosystem function, a body of theory known as *modern coexistence theory* has provided a general framework for understanding and predicting the maintenance of diversity itself. As a quantitative currency for coexistence, the theory identifies two processes: *stabilization*, which helps all species to resist competitive exclusion by reducing their relative negative effects on each other (and thus is also termed *niche difference*), and *equalization*, which reduces competitive imbalances between species (termed *fitness differences*) such that stabilization can ensure coexistence (Chesson, 2000; Ke & Letten, 2018). In contrast to the additive partition approach, which was developed to test empirical hypotheses in biodiversity–ecosystem function experiments (Loreau & Hector, 2001, 2019; Wagg et al., 2019), modern coexistence theory was first proposed to provide mechanistic predictions of coexistence in theoretical models (Chesson, 2000). Indeed, its metrics have successfully been applied to predict how a variety of specific biological mechanisms contribute to coexistence in theoretical (Letten et al., 2017; Yamamichi et al., 2022) and empirical studies (Godoy & Levine, 2014; Johnson et al., 2022;

Petry et al., 2018). Accordingly, studies have related niche and fitness measures from modern coexistence theory to ecosystem function (Carroll et al., 2011; Turnbull et al., 2013), though subsequent debate has questioned the generality and applicability of this approach (Loreau et al., 2012; Wagg et al., 2019). Thus, despite calls to adopt a more mechanistic view of biodiversity–ecosystem function relationships (Ratcliffe et al., 2017; Wang et al., 2024) and recent work comparing these relationships to niche and fitness metrics (Godoy et al., 2020), there is no general framework extending the predictive power of modern coexistence theory to address communities' total function.

Building upon this emerging interchange, this Concepts and Synthesis article aims to quantitatively bridge modern coexistence theory and biodiversity–ecosystem function research. Despite the two fields' differing aims, historical development, and terminology, summarized in Box 1, we highlight fundamental connections between species coexistence and ecosystem functioning. Our proposed quantitative framework, which we term *functional coexistence theory*, extends modern coexistence theory to highlight the importance of considering species' functional imbalances in tandem with their classical niche and fitness differences. Integrating these components with mechanistic models and experiments, researchers can quantify the biological processes governing coexistence between species in order to quantitatively predict community function. First, we use classic competition models to illustrate our framework (section *Linking coexistence and ecosystem function: functional coexistence theory*). Our simple graphical framework highlights the fundamental link between species coexistence and ecosystem function, mediated by three processes determining the total function of a community: stabilizing niche difference, fitness–function relationships, and functional equalization. Next, we place our functional coexistence framework within the context of the rich literature on biodiversity–ecosystem function to show that the two approaches are compatible despite their quantitative differences (section *Placing functional coexistence theory in the context of biodiversity–ecosystem function research*). Finally, we demonstrate how our theory can synthesize coexistence and ecosystem function research by presenting three case studies (section *Applying functional coexistence theory to theoretical and empirical systems*), applying functional coexistence theory to (1) theoretical consumer–resource models, (2) empirical data from competition experiments, and (3) recent questions of ecosystem multifunctionality. We conclude by outlining a path to closer synthesis between coexistence and diversity–function research (section *Conclusion: synthesizing community and ecosystem perspectives in a changing world*). By quantitatively identifying biological processes and ecological tradeoffs underpinning diversity–function relationships, our results can help better predict how ecosystems, along with the key services they provide, will respond to change.

LINKING COEXISTENCE AND ECOSYSTEM FUNCTION: FUNCTIONAL COEXISTENCE THEORY

In this section, we illustrate how modern coexistence theory's niche and fitness measures can be integrated with measures of species' function in order to predict ecosystem function, beginning with a quantitative two-species framework frequently employed in empirical studies of coexistence. Just as modern coexistence theory classifies the processes affecting coexistence (section *Modern coexistence theory: two components maintaining diversity*), our framework, termed *functional coexistence theory*, aims to classify components contributing to the total function of communities. We illustrate this by deriving conditions promoting total biomass in the two-species Lotka–Volterra model (Box 2), focusing specifically on *transgressive overyielding* (see Box 1, item 2c.i), which occurs when a community's total function exceeds that of its most productive species (Loreau, 1998; Trenbath, 1974). We find simple mathematical and graphical conditions for transgressive overyielding, allowing us to introduce the three processes promoting ecosystem function under functional coexistence theory (section *Functional coexistence theory: three components driving transgressive overyielding*). Furthermore, because transgressive overyielding is the most stringent of commonly applied *measures of biodiversity effects* (Box 1, item 2c), these results also serve as a starting point for understanding a variety of other metrics for biodiversity effects and existing empirical work on their drivers (section *Integrating niche, fitness, and function to predict ecological outcomes*).

Modern coexistence theory: Two components maintaining diversity

Modern coexistence theory highlights that differences between species can affect coexistence in two ways: they may promote coexistence by helping all species in a community to invade (i.e., resist competitive exclusion), or hinder coexistence by creating competitive imbalances favoring certain species over others. Accordingly, species coexistence can be predicted from two metrics summarizing these roles: niche differences (ND) promote coexistence, while fitness differences (FD) hinder coexistence. Stated conceptually, coexistence occurs when niche differences are greater than fitness

BOX 1 Coexistence and ecosystem function: Key outcomes and metrics

In this synthesis, we aim to highlight fundamental connections between species coexistence and ecosystem function. Despite increasing interchange (Godoy et al., 2020; Wang et al., 2024), the modern coexistence theory and biodiversity–function research programs have had separate historical developments and overarching aims (Wagg et al., 2019). Accordingly, the terminology from each field may be unfamiliar to nonspecialists. Moreover, even related ideas between fields may differ subtly in scope. To help bridge this divide, we outline the key outcomes and metrics of each framework, providing our chosen mathematical notation where applicable. Each framework considers an *ecological outcome* based on some *species-level measurement* and defines *system-level metrics* to summarize the underlying processes affecting the outcome of interest.

1. **Modern coexistence theory**—a framework which aims to identify the processes responsible for the *maintenance of diversity* (recently reviewed by, e.g., Barabás et al., 2018; Godwin et al., 2020) by allowing all species to *persist* in a community. This means that it considers the long-term dynamics of a system of interacting species, independently of the rate at which the community approaches this outcome or the duration of any experiments used to parameterize the dynamics.

1a. Outcome: **species persistence**—whether a given species will remain present at positive abundance in a community over long time periods (Kang & Chesson, 2010). *Coexistence* occurs when all species in a community can persist.

1b. Species-level measurement: **invasion-based fitness**, F_i—a species' ability to persist under competition, as measured through *invasion analysis*, with appropriate mathematical scaling (Appendix S1: Section S1); hence, this can also be termed a *scaled invasion growth rate*. We use the capital letter F to highlight that it is the underlying "common currency" of *fitness* in modern coexistence theory (Grainger et al., 2019).

1c. System-level metrics: **coexistence components**—two metrics that describe species persistence across the community. These can be defined in multiple ways (Spaak et al., 2023); here, we choose the most widely applied set of definitions (Chesson & Kuang, 2008), which can be directly calculated from invasion-based fitness (Carroll et al., 2011).

1c.i. **(Stabilizing) niche differences**, ND—the strength of negative feedbacks that maintain coexistence by helping all species to persist (i.e., by increasing all species' invasion-based fitness). Increasing niche difference, also known as *stabilization*, promotes coexistence. Here, we use $\mathrm{ND} = -\log\rho$, where ρ is the classically defined *niche overlap*.

1c.ii. **Fitness difference**, FD—the difference between various species' abilities to persist (i.e., their imbalance in invasion-based fitness). Decreasing fitness difference (known as *equalization*) therefore promotes coexistence. Here, we use $\mathrm{FD} = \log f_i/f_j$, where f_i/f_j is the classically defined *fitness ratio* between species i and j. The symbol f is only defined as part of the ratio f_i/f_j, for a species pair, unlike F_i, which is invasion-based fitness at the species level. We contrast lower and upper case symbols to emphasize that both quantities measure fitness, but do so in slightly different ways.

2. **Biodiversity–ecosystem function**—or in short, *diversity–function*—a research program (recently reviewed in, e.g., Barry, Mommer, et al., 2019; O'Connor et al., 2022) that aims to identify how differences in diversity (e.g., number of species) affect a community's total degree of *ecosystem function*, giving rise to differences known as *biodiversity effects*. It treats a different temporal scale: instead of the community's long-term state, studies typically focus on the outcome at a defined time point (often, the duration of an experiment or the time scale of global change).

2a. Outcome: **ecosystem function**—the degree to which an ecosystem exhibits some property of interest, related to the stock or flow of energy or materials (e.g., biomass production, our main example here).

2b. Species-level measurement: **yield**, Y_i—the level of ecosystem function a species exhibits at a time point of interest, typically at the end of an experiment.

2b.i. **Monoculture yield**—the yield of a species when grown alone (also termed *yield in isolation*). We denote this K_i for biomass and Φ_i for other functions.

2b.ii. **Mixture yield**—the yield of a species within a community (also termed *observed yield*). We denote this N_i for biomass and Y_i for other functions ($\widehat{N}_i, \widehat{Y}_i$ when these are evaluated at equilibrium).

2b.iii. **Total (mixture) yield**—the sum of all species' yields in a community.

2c. System-level metrics: **measures of biodiversity effects**—various metrics comparing mixture yield to some baseline across the community, indicating whether diverse communities outperform monocultures. Without further qualification, *biodiversity effect* sometimes refers to the *difference from expected yield* metric ΔY, but here, we use "biodiversity effects" only in the general sense. Many of these metrics have also been termed *overyielding* (Hooper & Dukes, 2004; Schmid et al., 2008; Trenbath, 1974).

2c.i. **Transgressive overyielding**—the degree to which total yield exceeds the monoculture yield of the best species. This can be viewed as a special case of the next, more general, metric.

2c.ii. **Difference from expected yield**, ΔY—the degree to which total yield exceeds some expected yield, calculated using a weighted average of monoculture yields. These weights are typically the starting proportions in an experiment. In theoretical studies (and some experiments), the weights are often equal, in which case, ΔY measures the degree to which the community *outperforms the average (monoculture) yield*. The *additive partition* of Loreau and Hector (2001) decomposes the ΔY metric into the following two components:

2c.iii. **Complementarity effect**, CE—an average indicating how much more species tend to yield in the community than growing alone, often attributed to resource partitioning or facilitation.

2c.iv. **Selection effect**, SE—a summary statistic measuring effects that depend on species identity, quantifying the tendency for higher yielding species to contribute more to the community. This can also be negative, indicating the presence of tradeoffs that reduce total yield (Jiang et al., 2008).

differences ($\text{ND} > |\text{FD}|$), allowing all species to attain positive invasion growth rates (Barabás et al., 2018). We depict these requirements for a two-species system in Figure 1a.

Thus, processes maintaining diversity can be classified according to these two components. The first, *stabilization*, increases niche differences (Figure 1a, blue arrow); to clarify their role in coexistence, niche differences are therefore sometimes termed *stabilizing niche differences*. The second, *equalization* (Figure 1a, orange arrows), makes species more similar in fitness, thereby reducing competitive hierarchy and preventing exclusion (Figure 1a, orange arrows). This stabilizing–equalizing framework does not directly quantify causative mechanisms because its components do not directly correspond to concrete biological processes (Barabás et al., 2018; Loreau et al., 2012; Song et al., 2019). However, applied to mechanistic models, it provides a powerful tool for summarizing how coexistence can arise through processes ranging from abiotic interactions such as nutrient uptake (Letten et al., 2017) to biotic interactions such as pollination (Johnson et al., 2022), mutualism (Kandlikar et al., 2019; Ke & Wan, 2023), or disease (Mordecai, 2011).

Functional coexistence theory: Three components driving transgressive overyielding

In Box 2, we extend modern coexistence theory in order to include ecosystem function by relating its niche and fitness measures to the total function of the community. As a representative example, we consider the conditions under which the community's biomass production shows *transgressive overyielding*; that is, when total biomass at equilibrium exceeds the monoculture biomass of the most productive species (Loreau, 2010). While we use the familiar Lotka–Volterra model as an illustration, our results rest upon a more general finding that in many models of competition, a species' relative abundance (and thus, its contribution to total yield) can be determined from two quantities: (1) its monoculture yield K_i, or biomass produced when growing alone, and (2) its invasion-based fitness F_i, or ability to persist under competition (Box 2: Equation 4; Appendix S1: Section S1). This includes, in addition to the Lotka–Volterra model used in Box 2, many models with nonlinear competitive responses such as the Beverton–Holt model (Beverton & Holt, 1957) used to study annual plant competition (Levine & HilleRisLambers, 2009) and Tilman's (1982) substitutable resource competition model (Letten et al., 2017). Indeed, empirical evidence also demonstrates that monoculture yield explains a large proportion of variation in mixture yield (Parker et al., 2019) and that this relationship can predict biodiversity effects (Crawford et al., 2021). Furthermore, this relationship is approximately true in an even broader class of theoretical models (Arnoldi et al., 2022), enabling further generalizations.

Using this result, we combine the niche and fitness measures from modern coexistence theory (here, ρ and f_1/f_2) with each species' monoculture yield (K_1, K_2) to fully predict total biomass and how it responds to

BOX 2 Linking coexistence to ecosystem function: Transgressive overyielding

For a class of commonly used competition models, we can use the niche and fitness components of modern coexistence theory to calculate total ecosystem function. In this Box, we provide a technical overview showing how to derive conditions for transgressive overyielding (given in full detail in Appendix S1: Section S1; conditions for other outcomes in Appendix S1: Section S2). These results are also introduced conceptually and illustrated using numerical simulations in the main text.

As a representative example, we use the classic Lotka–Volterra model. Species i's population N_i obeys the ordinary differential equation for per capita growth rate

$$\frac{1}{N_i}\cdot\frac{dN_i}{dt}=r_i\cdot\left(1-\sum_j \alpha_{\mathrm{ij}}N_j\right), \tag{1}$$

where r_i is species i's intrinsic rate of increase and α_{ij} is the per capita competitive effect of species j on species i. Note that we discuss biomass here for simplicity, but that results are fully analogous for any function Φ instead of biomass K, as discussed in Appendix S1: Section S7.

Modern coexistence theory: niche and fitness measures: In a two-species community, the niche and fitness components are as per Chesson and Kuang (2008),

$$\rho=\sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}}\ \text{and}\ \frac{f_1}{f_2}=\sqrt{\frac{\alpha_{21}\alpha_{22}}{\alpha_{12}\alpha_{11}}}, \tag{2}$$

which respectively give the *niche overlap* and *fitness ratio* between species 1 and 2. Two conditions allow the species to coexist stably, each corresponding to one of the coexistence components in modern coexistence theory. First, species must experience niche differentiation: $\rho<1$, ensuring that within-species competition is stronger than between-species competition. Second, species must be sufficiently similar in competitive ability:

$$\rho<\frac{f_1}{f_2}<\rho^{-1}, \tag{3}$$

ensuring that the fitness ratio between species is not too imbalanced relative to niche differentiation. Since ρ and f_1/f_2 are ratios, we can take logarithms to obtain niche and fitness differences corresponding to the conceptual discussion in the section *Modern coexistence theory: two components maintaining diversity* ($\mathrm{ND}=-\log\rho$ and $\mathrm{FD}=\log f_1/f_2$; Johnson et al., 2022; Yamamichi et al., 2022), where coexistence requires $\mathrm{ND}>|\mathrm{FD}|$. We illustrate these coexistence conditions in Figure 1a, a semi-logarithmic plot with f_i/f_j plotted on a log-scale y-axis, as commonly depicted in the literature.

Fitness determines species' contributions to total yield: To link these measures to function, we first focus on *mixture yield* $\widehat{N}_i$, the biomass that species i contributes to the community, assuming the system is at equilibrium. We find that this is proportional to its *monoculture yield* $K_i=\alpha_{ii}^{-1}$ (i.e., carrying capacity) and to a quantity we term its *invasion-based fitness* $F_i=1-\alpha_{ij}/\alpha_{jj}$ (i.e., *invasion growth rate* scaled by r_i). This gives a straightforward expression for biomass of species i at equilibrium,

$$\widehat{N}_i=\frac{F_iK_i}{1-\rho^2}. \tag{4}$$

In conceptual terms, the higher invasion-based fitness F_i a species has under competition, the more it contributes to the community relative to its monoculture yield, according to a proportionality constant that depends on niche overlap ρ.

Invasion-based fitness (F_i) vs. fitness ratio (f_i/f_j): Here, as in more general versions of modern coexistence theory (Barabás et al., 2018), F_i measures a species' fitness—its ability to persist under competition with the rest of its community. We apply F_i to simplify the derivation of our results and emphasize their link to *invasion analysis*, the powerful and highly generalizable basis of modern coexistence theory (Grainger et al., 2019). The traditionally defined fitness ratio f_1/f_2 quantifies two species' imbalance in F_i as $\sqrt{(1-F_2)/(1-F_1)}$ and niche overlap ρ quantifies competitive reduction in both species' F_i as $\sqrt{(1-F_1)(1-F_2)}$ (Carroll et al., 2011). Unlike invasion-based fitness F_i, the symbol f only occurs as a ratio. We contrast lower and upper case letters to highlight that the quantities are related (but not identical) measures of fitness. Importantly, we can relate the two sets of quantities using the identity

$$F_i = 1 - \rho \cdot f_j / f_i, \tag{5}$$

which shows that as the fitness ratio increasingly favors species i, its invasion-based fitness F_i also increases.

Effects on total yield: Using Equation (4) to write total yield (biomass) as $\widehat{N}_1 + \widehat{N}_2 = (F_1K_1 + F_2K_2)/(1-\rho^2)$, we can relate changes in total biomass (and hence transgressive overyielding) to the niche and fitness components derived above. Without loss of generality, we designate species 1 as the higher yielding species in monoculture ($K_1 > K_2$). Transgressive overyielding occurs when total biomass exceeds K_1; accordingly, we rewrite this equation as:

$$\hat{N}_1 + \hat{N}_2 = K_1 \cdot \frac{F_1 + \frac{K_2}{K_1} \cdot F_2}{1-\rho^2}, \tag{6}$$

This precisely predicts how total biomass depends on niche overlap ρ, invasion-based fitness F_i, and monoculture yield K_i. We will explore these relationships more extensively below and in the main text (*Functional coexistence theory: three components driving transgressive overyielding*). However, merely by examining the equation, it is possible to note that there are three ways to change the value of Equation (6) relative to K_1, the baseline for transgressive overyielding: (1) changing *stabilization*, that is, how close ρ is to 0; (2) changing *fitness imbalance*, that is, the relative magnitudes of F_1 and F_2 for a particular value of ρ; and (3) changing *yield imbalance*, that is, how close the yield ratio K_2/K_1 is to 1. Note that these components are not fully independent due to the relationship between ρ, F_1, and F_2.

Conditions for transgressive overyielding: We are now ready to derive simple conditions for transgressive overyielding. Solving the conditions under which total biomass (Equation 6) is greater K_1 (and rewriting ρ in terms of F_1, F_2) gives $F_1 > 1 - K_2/K_1$. In other words, transgressive overyielding requires the higher yielding species to also have sufficiently high invasion-based fitness relative to its advantage in yield—a *fitness–function relationship*. This ensures that the higher yielding species is abundant in the community. Rewriting this in terms of ρ and f_1/f_2 (Appendix S1: Section S1) gives the *functional coexistence theory* condition for transgressive overyielding:

$$\rho \cdot \frac{K_1}{K_2} < \frac{f_1}{f_2} < \rho^{-1}, \tag{7}$$

where $K_1/K_2 > 1$, and the upper bound of ρ^{-1} is due to the fact that coexistence is a prerequisite for transgressive overyielding. As niche overlap ρ decreases (i.e., species experience increasing niche difference), transgressive overyielding first becomes possible when $\rho \cdot K_1/K_2 = f_1/f_2 = \rho^{-1}$ and thus at

$$\frac{f_1}{f_2} = \sqrt{\frac{K_1}{K_2}}, \tag{8}$$

which is also the fitness ratio maximizing total biomass (i.e., the optimal fitness ratio such that bringing f_1/f_2 toward this value would promote transgressive overyielding; shown in Appendix S1: Section S1).

Excess niche and fitness differences: Illustrated in Figure 1b, the transgressive overyielding condition (Equation 7) is closely related to the coexistence condition from modern coexistence theory (Equation 3). In fact, using the conceptual notation from section *Modern coexistence theory: two components maintaining diversity* to rewrite Equation (7), transgressive overyielding requires

$$\mathrm{ND}-\Delta > |\mathrm{FD}-\Delta|, \tag{9}$$

where ND, FD are defined logarithmically as above, and $\Delta = \frac{1}{2}\log K_1/K_2$ (the logarithm of Equation 8) measures the yield imbalance to be overcome (Appendix S1: Section S1). Simply put, Equation (9) states that transgressive overyielding requires that niche difference and the higher yielding species' fitness advantage are in excess of requirements for coexistence. Meanwhile, the expression for Δ means that a greater difference in yield must be overcome by even stronger excess niche and fitness differences. Graphically, this means that greater Δ results in a larger mismatch between the parameter region for coexistence (dark gray) and transgressive overyielding (green; shifted toward the upper-right direction) in Figure 1, while bringing the optimal fitness ratio (Equation 8; dashed line in Figure 1b) closer to one results in a greater overlap.

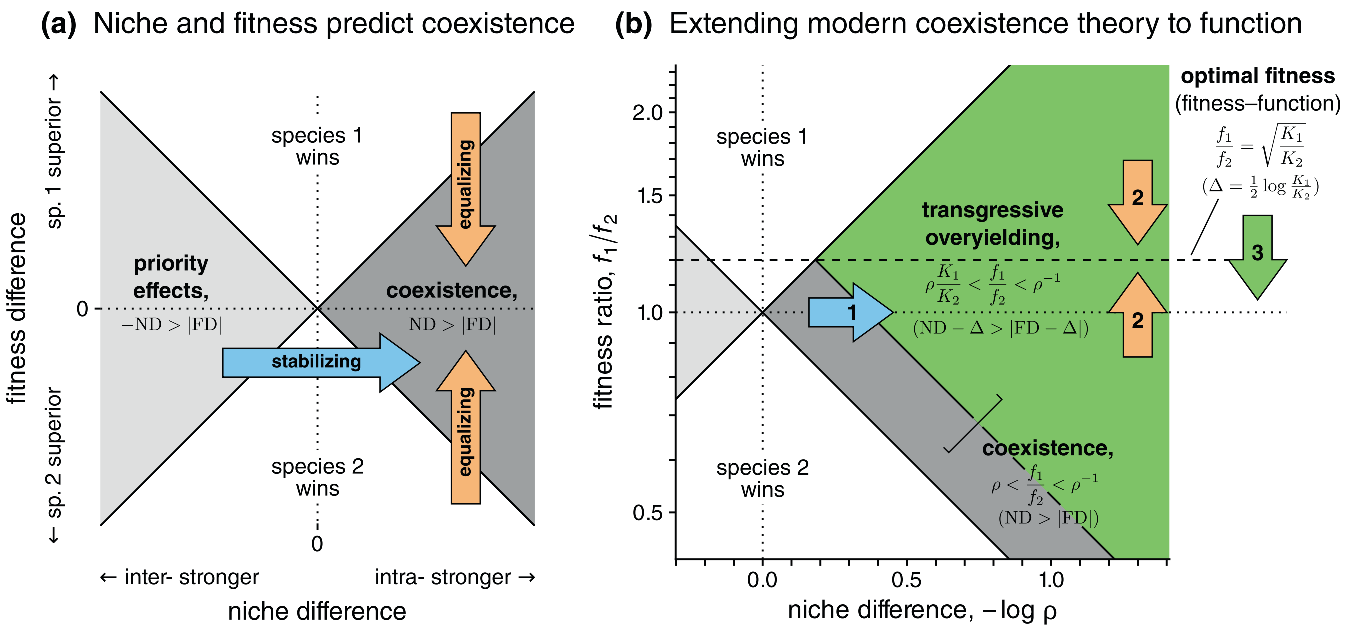


FIGURE 1 Modern coexistence theory and its functional extension. (a) Modern coexistence theory: Niche and fitness differences predict coexistence. Coexistence outcomes between two species depend on niche difference, ND (horizontal axis), and fitness difference, FD (vertical axis; panel adapted from Mordecai, 2011). Coexistence (dark gray) requires niche difference to be positive and large enough to overcome fitness difference (ND > |FD|). Any process promoting coexistence can be partitioned into two components: Stabilizing (blue arrow), that is, increasing niche difference, and equalizing (orange arrows), that is, decreasing the magnitude of fitness difference toward zero. Here, ND and FD are notated conceptually, but can be quantified for specific models, as discussed below. (b) Functional coexistence theory: Extending the modern coexistence framework to predict function. We now use niche and fitness measures to predict whether species interactions cause a community's total biomass to be greater than that of its best single species, termed *transgressive overyielding*. Here, these are defined as $\mathrm{ND} = -\log\rho$ and $\mathrm{FD} = \log f_1/f_2$, where ρ is the niche overlap and f_1/f_2 is the fitness ratio (note logarithmic scale) between the two species, and log denotes the natural logarithm. Transgressive overyielding (green region) only occurs when the higher yielding species (here, species 1) also has sufficiently high fitness ($\rho \cdot K_1/K_2 < f_1/f_2 < \rho^{-1}$) or equivalently, when niche difference and 1's fitness advantage are in excess of those required for coexistence ($\mathrm{ND}-\Delta > |\mathrm{FD}-\Delta|$, where $\Delta = \frac{1}{2}\log(K_1/K_2)$). Accordingly, processes promoting function can be partitioned into effects on niche (blue arrow 1, increasing niche differences) and fitness (orange arrows 2, bringing f_1/f_2 toward the value representing the optimum fitness–function relationship; dashed line), as previously, but also on functional imbalance between the species (green arrow 3, showing the optimal value [dashed line] approaching $f_1/f_2 = 1$).

community coexistence (Box 2: Equation 7). We identify three processes that enable transgressive overyielding (Loreau, 2010), as depicted in Figure 1b. The first is simply stabilizing niche differences: increasing niche difference (decreasing ρ toward zero) tends to increase total biomass (arrow 1). The second concerns the relationship between fitness and function: transgressive overyielding occurs when the higher yielding species has a competitive advantage in excess of that needed for it to persist (arrow 2). The third component can be termed *functional equalization*: making the species more similar in monoculture yield (decreasing K_1/K_2 toward 1) increases the potential for transgressive overyielding (arrow 3). In this section, we simulate how these components affect total biomass in the Lotka–Volterra model (Figure 2) and use these results to illustrate the interpretation of each process.

Component 1: stabilizing niche differences

In the pairwise models we consider, niche difference (and equivalently, stabilization) can be interpreted as the tendency for intraspecific interactions to be more negative than interspecific ones: that is, for species to limit themselves more strongly than they limit each other. Confirming previous results (Carroll et al., 2011), we find that such niche differences tend to promote total yield (Figure 2a). However, we caution that functional and competitive imbalances can complicate this relationship: when the higher yielding species had only moderately higher fitness advantage than its competitor ($f_1/f_2 = 1.03$ and 1.13), increasing niche difference just enough to allow coexistence decreased total biomass. Thus, transgressive overyielding generally requires niche differentiation in excess of that simply required for coexistence (e.g., Figure 1b, where the boundary for transgressive overyielding lies to the right of the coexistence boundary). Nonetheless, regardless of the fitness ratio between coexisting species, sufficiently high niche differences always eventually enabled transgressive overyielding. Accordingly, we follow previous work in emphasizing that niche differentiation plays an essential role in allowing diversity to promote ecosystem function.

Component 2: fitness–function relationship

Modern coexistence theory highlights the role of *invasion-based fitness* (F_i; Box 1, item 1b) and derived measures (e.g., f_i/f_j) in determining the ability for species to persist in a community. Indeed, without the context provided by fitness measures, predicting coexistence is impossible (Adler et al., 2007; Kandlikar et al., 2019). Going further, our functional framework highlights that fitness also determines the degree to which each species contributes to total ecosystem function. We find that transgressive overyielding requires precise relationships between fitness and function: namely, a species with higher function (here, monoculture yield in biomass K) must also have a sufficiently high competitive ability (as measured by F_i or f_i/f_j; Figure 2b). In other words, higher functioning species must have fitness in excess of that required for coexistence (by a factor of K_1/K_2; Equation 7). Our simulations highlight that this component can be viewed as a version of modern coexistence theory's equalization: regardless of niche difference, bringing fitness ratio toward its optimum value (vertical dashed line, $\sqrt{K_1/K_2}$; Equation 8) always promoted transgressive overyielding, just as bringing it toward 1 would have promoted coexistence. Thus, our functional framework generalizes modern coexistence theory by showing that fitness measures also determine ecosystem function.

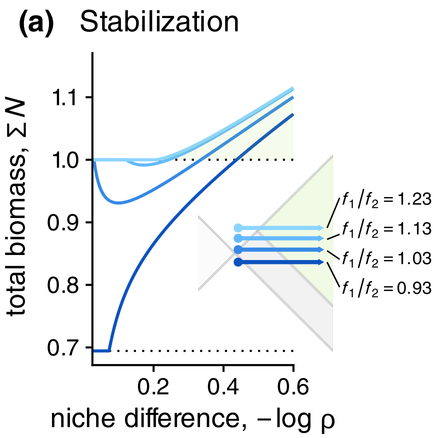
Component 3: functional equalization

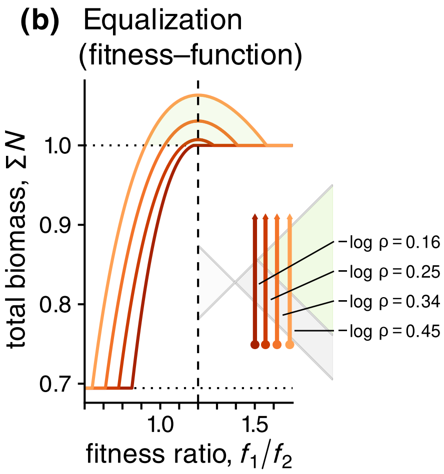
Finally, we identify a driver of diversity–function relationships with no direct equivalent from modern coexistence theory: functional equalization, which increases ecosystem function by reducing functional imbalances between species (e.g., low vs. high biomass production). As our simulations illustrate (Figure 2c), making coexisting species more equal in function always promotes transgressive overyielding because it reduces the opportunity for competition to select (i.e., increase the relative abundance of) functionally inferior species (i.e., the gray region in the inset becomes smaller). Functional equalization amplifies the effect of stabilizing niche differences. As an example, we might consider the case where species have equal function ($K_1 = K_2$). This causes the conditions for transgressive overyielding (Equation 7) to exactly match those for coexistence—that is, transgressive overyielding always occurs as a consequence of stable coexistence. In this extreme, the previous fitness–function relationships become irrelevant because species do not differ in function, a scenario implicitly considered by classic experimental analyses designed for communities where species have similar monoculture yields (e.g., the relative yield total approach: De Wit, 1960). While functional imbalance has been discussed as a caveat for the interpretation of such studies (Schmid et al., 2008; Wagg et al., 2019), it has received little attention as an explanation of biodiversity effects in its own right; thus, we highlight its importance in predicting the total function of a community.

Integrating niche, fitness, and function to predict ecological outcomes

While our results in Box 2 focus on the simple case of transgressive overyielding, functional coexistence theory can provide more general quantitative insight into the drivers of ecosystem function. The rules for transgressive overyielding are closely related to overall patterns in ecosystem function, as we show in Figure 3a by plotting total biomass on the space defined by the niche (*x*-axis) and fitness (*y*-axis) components. Indeed, the conditions for transgressive overyielding and for other measures of positive biodiversity effects can be viewed as special cases of the same general conditions (contour lines in Figure 3a). Put simply, our results extend to any total yield-based measure that compares the community's total yield to an expected yield. For instance, we can predict the conditions that allow a community to outperform the average monoculture yield (Figure 3a: solid line and green shaded region; see also Appendix S1: Section S2 for generalization to any expected yield). As before, the community outperforms some expected yield when (1) stabilizing niche differences and (2) the fitness advantage of the higher yielding competitor is in excess of the requirements for coexistence, where (3) the required fitness advantage increases with the degree of imbalance between species' monoculture yields. Thus, our niche, fitness, and function components provide a general approach to categorizing the potentially complex effects of species interactions on a community's total function.

In many cases, our framework synthesizes well-supported patterns from the population, community, and ecosystem ecology literature. Corresponding to our first component (*stabilizing niche differences*), the role of niche partitioning in promoting the total function of a community has long been theoretically understood (Loreau, 2004; MacArthur, 1970; Turnbull et al., 2013), and tests of this hypothesis using empirical proxies of niche partitioning have often found the expected positive effects on productivity and function, for instance in forest ecosystems (Liang et al., 2015; Williams et al., 2017).


(a) Stabilization


(b) Equalization (fitness–function)

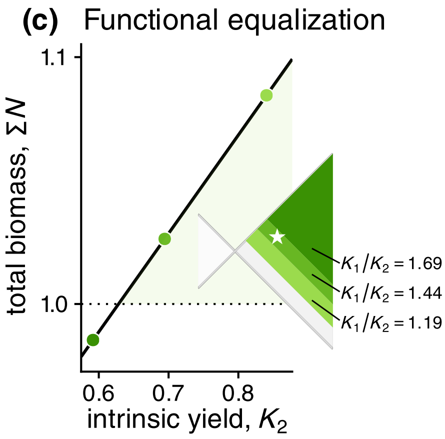

(c) Functional equalization

FIGURE 2 Illustrating causes for transgressive overyielding using the Lotka–Volterra model. In each panel, we show the effect (solid lines/points) of varying a component (horizontal axis) on total biomass (vertical axis) as compared to the biomass of each species growing alone (dotted horizontal lines; set to 0.7 for the less productive species 2 and 1.0 for the more productive species 1). Insets show parameter values and positions on the coexistence space plot in Figure 1b. (a) Stabilizing niche differences. Increasing niche difference $1-\rho$ eventually results in transgressive overyielding, regardless of fitness difference (line color). Note that the line for $f_1/f_2 = 1.23$ overlaps or is slightly above that for $f_1/f_2 = 1.13$. (b) Fitness–function relationship. Transgressive overyielding occurs when bringing f_1/f_2 toward the value representing the optimum fitness–function relationship $f_1/f_2 = \sqrt{K_1/K_2} = 1.2$ (vertical dotted line), provided niche difference (line color) is high enough to allow coexistence at this fitness ratio. (c) Functional equalization. Making species more equal in function by increasing the productivity of the inferior species K_2 while niche and fitness remain fixed (star in inset) increases total biomass by increasing the potential for transgressive overyielding (different green regions in inset). See Appendix S1: Section S8 for parameter values.

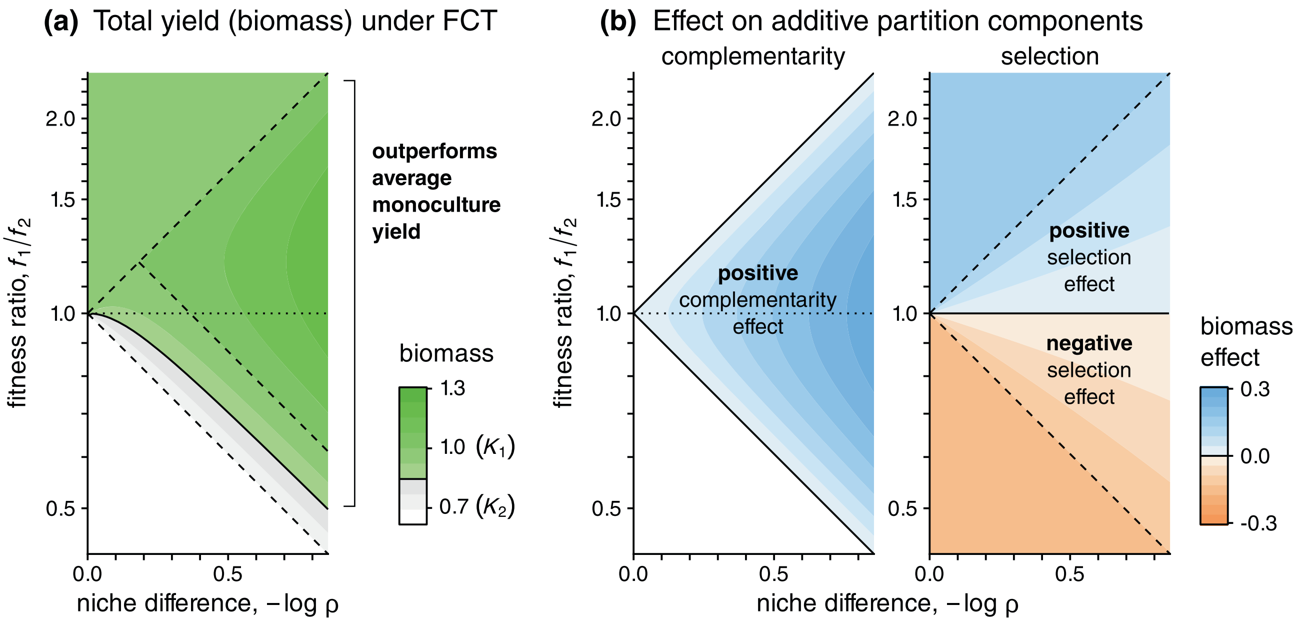


FIGURE 3 Different outcomes and measures of biodiversity effects under functional coexistence theory (FCT). Axes are those of Figure 1b, with niche difference on the x-axis and fitness ratio (log scale) on the y-axis. (a) Total yield. We plot contours showing the total biomass of the community at equilibrium. Darker colors show increasing biomass, starting from the biomass of the lower yielding species (white), and values greater than the average monoculture yield $(K_1+K_2)/2$ are shown in green. This reveals the boundary above which fitness ratio is sufficient for the community to outperform average yield (black line), which lies between the original coexistence and transgressive overyielding boundaries (dashed lines). (b) Additive partition components. We show similar contour plots for the additive partition components. The color scale is shared between components and is in units of biomass. Complementarity (left) is always positive (blue) within the coexistence region (solid lines), while the sign of selection (right) depends on the boundary $f_1/f_2=1$ (solid line): Positive when species 1 (the species with higher monoculture yield) has higher fitness, but negative (red) when species 2 has higher fitness.

Similarly, our second component, the *fitness–function relationship*, has well-established precedents in the literature. For instance, the *Montgomery effect* (Gustafsson, 1951; Montgomery, 1912), known from agricultural experiments for over a century, stresses tradeoffs where species with high yield in isolation perform poorly in competition, reducing the productivity of mixed communities. A wealth of evidence has subsequently demonstrated the importance of understanding the relationship between species' performance in isolation and under competition (Jiang et al., 2008). In one recent case, Crawford et al. (2021) showed that the correlation between species' biomass in monoculture and mixture could effectively predict the direction of diversity–function relationships.

Meanwhile, our third component, *functional equalization*, points to new directions for ecosystem function research by suggesting that functional imbalance (i.e., productivity variation) across the community could be a direct driver of ecosystem function. While functional variation has indeed received increasing attention in the biodiversity–ecosystem functioning literature, the focus to date has been on applying functional trait variation as a proxy for interspecies competitive processes creating niche differentiation (Finegan et al., 2015; Flynn et al., 2011; Huxley et al., 2023; Liu et al., 2024) or competitive hierarchy (Cadotte, 2017; Huang et al., 2020). Our new synthesis suggests that in addition to these roles, such variation could also directly harm total function by contributing to an imbalance in species' monoculture yield across the community. Indeed, Roscher et al. (2005) found weaker overyielding in a community of 60 ecologically diverse plants than in a 9-species subset of "dominant" strategists sharing high expected monoculture biomass. Similarly, Cadotte (2017) and Huang et al. (2020) found that greater variation in height, a key determinant of plants' ability to access limiting resources (light), was associated with reductions in total biomass. Accordingly, we propose that integrating the niche, fitness, and function components from our theory could provide new ways to summarize and predict diversity–function relationships.

PLACING FUNCTIONAL COEXISTENCE THEORY IN THE CONTEXT OF BIODIVERSITY–ECOSYSTEM FUNCTION RESEARCH

Although previous work has used concepts from modern coexistence theory to examine questions from the biodiversity–ecosystem function literature, it has remained unclear whether these two approaches can be reconciled. In this section, we place functional coexistence theory within the context of the existing literature in order to show how it complements previous approaches. Much of the previous quantitative work on the connections between coexistence and ecosystem function has focused on the two components of Loreau and Hector's (2001) *additive partition* of biodiversity effects. Thus, we briefly summarize the interpretation of the additive partition's complementarity and selection components: though their respective links with niche and fitness have long been noted, the broader compatibility of the two frameworks has remained contentious (section *Previous attempts to synthesize diversity–function relationships and coexistence*). After quantitatively relating niche and fitness measures to the complementarity and selection components (Box 3), we highlight how the perspective of functional coexistence theory resolves apparent contradictions between the theories (section *Comparing the functional coexistence theory and additive partition frameworks*). Finally, we return to the broader goal of predicting ecosystem function in a changing world and highlight how functional coexistence theory can supplement previous approaches in identifying the biological processes (i.e., mechanisms) responsible for diversity–function relationships (section *Identifying mechanisms linking biodiversity and ecosystem function*).

Previous attempts to synthesize diversity–function relationships and coexistence

The links between productivity and the processes allowing species to coexist have been noted since early efforts to quantify competition (De Wit, 1960), culminating in quantitative descriptions of niche partitioning between species (e.g., MacArthur, 1970). Building upon this perspective, studies from the biodiversity–ecosystem function literature (reviewed in Hooper et al., 2005) have hypothesized that such niche partitioning effects may explain widely observed positive effects from diversity manipulation experiments. To synthesize the diversity of metrics and hypotheses from this field, Loreau and Hector (2001) proposed the *additive partition* of such biodiversity effects into two components. The first, *complementarity*, is an average indicating how much more species tend to yield in communities than growing alone, which can serve to quantify the role of niche partitioning and other interactions such as facilitation (Hooper et al., 2005; Loreau, 2004; Loreau et al., 2012; Turnbull et al., 2013). The second component, *selection*, measures effects that depend on species identity by quantifying the tendency for species with higher monoculture yield to contribute more to communities (Fox, 2005; Loreau, 1998). A positive value of this component indicates that selection for higher yielding species increases total yield, while a negative value means that lower yielding species are actually favored, a tradeoff which reduces total yield (Jiang et al., 2008). As Loreau and Hector (2001) originally suggested (and later refined by Fox, 2005), this selection component measures competitive differences in a manner analogous to fitness in evolutionary studies (Price, 1995). Thanks to its generality, the additive partition has successfully summarized a large and diverse set of experimental studies (Cardinale et al., 2011). Nonetheless, as long noted (e.g., Hooper et al., 2005; Loreau & Hector, 2001; Mouquet et al., 2002), it does not identify specific biological processes driving biodiversity effects, nor does it predict how they might change with respect to time or environmental context.

More recent work has suggested that modern coexistence theory may help address limitations of the additive partition by helping to detect the biological mechanisms responsible for biodiversity effects (Carroll et al., 2011; Godoy et al., 2020; Turnbull et al., 2013; Wang et al., 2024). Indeed, the framework formalizes the same ecological concepts as the additive partition: like complementarity, niche difference measures processes reducing the importance of competition between species; like selection, fitness measures processes favoring one species over another (Adler et al., 2007). Accordingly, theoretical work has aimed to relate the approaches (Turnbull et al., 2013). Toward this goal, Carroll et al. (2011) suggested that the additive partition may misrepresent underlying mechanisms (e.g., resource partitioning), and proposed using niche difference as an alternative metric for diversity–function studies. However, a subsequent exchange questioned whether either approach appropriately indexes underlying mechanisms (Carroll et al., 2012; Loreau et al., 2012), while more recent debate (Loreau & Hector, 2019; Pillai & Gouhier, 2019) has stressed their different and potentially incompatible conceptual aims (Wagg et al., 2019). Thus, despite recent calls to harness ecological theory to identify mechanisms underlying diversity–function relationships (Barry, de Kroon, et al., 2019; Godoy et al., 2020; Ratcliffe et al., 2017; Wang et al., 2024), it remains unclear how to integrate the general insights offered by modern coexistence theory with standard approaches in the field of biodiversity–ecosystem function.

BOX 3 Relating functional coexistence to other frameworks for diversity effects

Loreau and Hector (2001) defined the *additive partition of biodiversity effects* by showing that ΔY, the difference between observed total yield and expected yield Y_E, can be written as

$$\Delta Y = \underbrace{n \cdot \overline{\Delta RY} \cdot \overline{K}}_{\text{complementarity, CE}} + \underbrace{n \cdot \mathrm{cov}(\Delta \mathrm{RY}, K)}_{\text{selection, SE}}, \tag{10}$$

where n is the number of species, K is monoculture yield or function when growing alone, RY_i is relative yield (a species' yield within the community divided by its monoculture yield), and $\overline{\cdots}$, $\mathrm{cov}(\cdots)$, and $\Delta\cdots$ respectively denote these quantities' mean, covariance, and deviation from experimenters' expectations. Expected yield is the weighted average of species' monoculture yields according to expected relative yields ($Y_E = \sum_i \mathrm{RY}_{E,i} K_i$); a typical choice of $\mathrm{RY}_{E,i}$ is species' proportions at the beginning of an experiment, but Equation (10) is valid for any choice of expected relative yield. Here, following previous studies (Carroll et al., 2011; Loreau, 2010), we consider changes relative to average monoculture yield $\overline{K}$ (corresponding to $\mathrm{RY}_{E,i} = 1/n$ and $Y_E = \overline{K}$).

Relating the additive partition to niche and fitness measures: We relate the additive partition to niche and fitness measures for Box 2's competition models (Appendix S1: Section S3) by considering the coexistence equilibrium. Noting that RY_i is our $\widehat{N}_i/K_i$, we find that complementarity is $\left[\sum F/(1-\rho^2) - 1\right] \cdot \overline{K}$, regardless of the choice of expected relative yield, and selection is $n \cdot \mathrm{cov}(F, K)/(1-\rho^2)$, provided all expected relative yields are equal, that is, $\mathrm{RY}_{E,i} = 1/n$. In this case, expected yield is simply average monoculture yield $\overline{K}$ and we can write these expressions out in full for the equilibrium abundances of (coexisting) species 1 and 2 as

$$\Delta Y = \Sigma \widehat{N} - \overline{K} = \underbrace{\frac{F_1 \cdot F_2}{1-\rho^2} \cdot \frac{K_1 + K_2}{2}}_{\text{complementarity, CE}} + \underbrace{\frac{F_1 - F_2}{1-\rho^2} \cdot \frac{K_1 - K_2}{2}}_{\text{selection, SE}}, \tag{11}$$

corresponding to previous results (Carroll et al., 2011; Loreau et al., 2012) except that we have greatly simplified the expression using invasion-based fitness F_1, F_2. As previously noted by Carroll et al. (2011), these expressions have complicated relationships with ρ and f_1/f_2; nonetheless, the form of Equation (11) suggests that complementarity is related to the tendency of both F_1 and F_2 to be large, while selection is related to the difference between F_1 and F_2. This implies that complementarity is analogous to niche difference and selection to fitness difference. We confirm these expectations using numerical simulations in Figure 4a–c; using Equation (5), we can also show them to hold exactly (Appendix S1: Section S3).

Comparing the functional coexistence theory and additive partition frameworks

In Box 3 (Appendix S1: Section S3), we calculate how complementarity and selection are related to the niche, fitness, and function components from functional coexistence theory, finding conceptual agreement between the frameworks despite quantitative differences. The contour plots in Figure 3b illustrate the general trends by indicating how the complementarity (left) and selection (right) components decompose variations in total yield (Figure 3a) for different values of the niche and fitness components. Using simulations (Figure 4a–c), we then explored these relationships in full by calculating the complementarity and selection components for the same scenarios originally simulated in Figure 2. Together, these serve to illustrate general theoretical relationships proven in Appendix S1: Section S3.

The effect of niche, fitness, and function on the additive partition

In our simulations, niche difference consistently and positively affected complementarity, but not selection. Indeed, when increasing niche difference (Figure 4a),

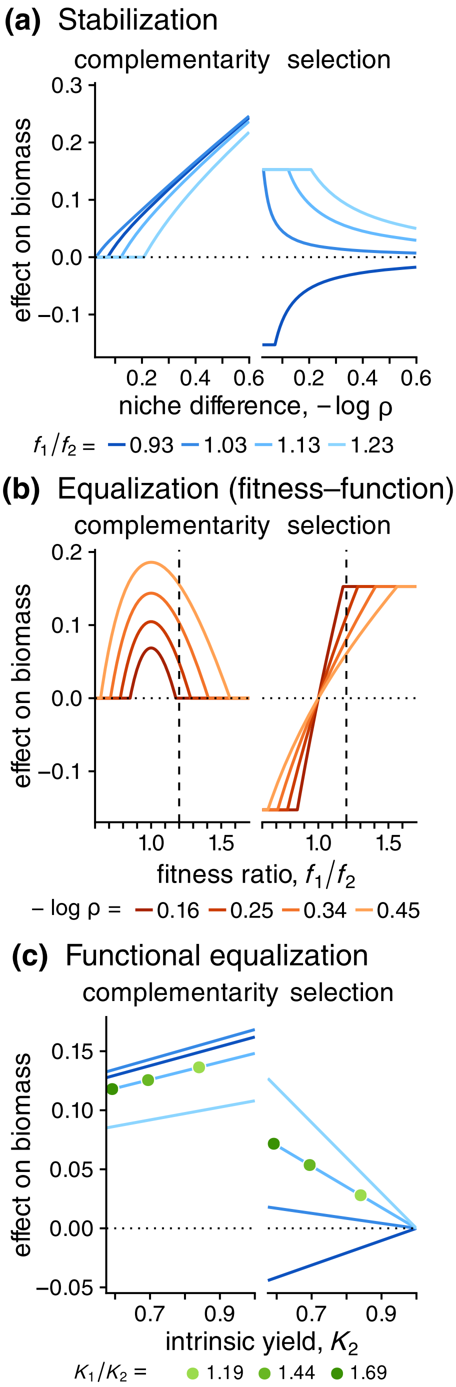


FIGURE 4 Relating (a) stabilization, (b) fitness–function, and (c) functional equalization to the additive partition. Following the simulations in Figure 2 (matching parameter values and legends), we show how each of the components of functional coexistence theory is related to the additive partition by using species' equilibrium biomass to calculate the complementarity (left) and selection effects (right) as in Box 3. Note that the calculations were performed by using the average monoculture yield as the expected yield. Instead of only showing one set of niche and fitness values (as in Figure 2c), panel (c) uses the same four values of f_1/f_2 (line color) as in panel (a).

complementarity (left) always increased regardless of the underlying fitness ratio (different blue lines). However, selection (right) either increased ($f_1/f_2 = -0.93$) or decreased (other values of f_1/f_2) depending on the underlying fitness ratio. Meanwhile, varying the fitness ratio consistently affected selection, but not complementarity. Namely, as we increased the fitness ratio (Figure 4b), selection (right) consistently increased regardless of the niche difference (different orange lines), and its sign always reflected the fitness hierarchy: negative when the fitness ratio favored the lower yielding species ($f_1/f_2 < 1$), and positive when it favored the higher yielding species ($f_1/f_2 > 1$; see also Figure 3b). In contrast, complementarity (left) increased and then decreased in response to increasing fitness ratio. Finally, yield imbalance affected the magnitude but not the sign of selection. Regardless of underlying niche difference (different blue lines), increasing the monoculture yield of the lower yielding species K_2 (i.e., functional equalization; Figure 4c) strongly decreased the magnitude of selection (right), which always reached zero when $K_2 = K_1 = 1$. This also slightly increased the magnitude of the complementarity (left) component, though this effect would disappear when standardizing by the average monoculture yield (see general result in Appendix S1: Section S3).

Analogies between modern coexistence theory and additive partition components

We conclude that the coexistence theory and additive partition components are closely linked: as previously suggested, complementarity is closely connected to stabilizing niche difference (Carroll et al., 2011; Loreau, 2004), and selection is related to fitness measures (Cadotte, 2017; Fox, 2005; Turnbull et al., 2016). Indeed, in the only direct experimental comparison of the additive partition and coexistence components, Godoy et al. (2020) showed matching changes in the two sets of metrics across environmental gradients. Our contour plots (Figure 3b) precisely support this analogy: complementarity (left) shows a consistent increase in the x- (niche) direction, while selection (right) consistently increases in the y- (fitness) direction. Accordingly, we suggest that one reason for the apparent mismatch (Carroll et al., 2011; Loreau et al., 2012) between the frameworks is that they quantify underlying niche differentiation in different ways. Even within modern coexistence theory, there are several ways to quantify niche and fitness (Spaak et al., 2023), and in fact, we can show that complementarity can be interpreted as an alternate niche difference metric (Appendix S1: Section S4), closely related to metrics based on arithmetic means of invasion growth rates (Chesson, 2003; Zhao et al., 2016).

A key difference: functional equalization modulates the importance of selection

Despite similarities between the two approaches, an obvious difference is that our framework has three parts, versus the classic additive partition's two components. More specifically, we identify that selection is closely related to two different kinds of imbalance: fitness difference and variation in monoculture yield (Figure 4b,c; also directly apparent in Equation 11), paralleling the role of monoculture yield in recent extensions of the additive partition itself (Isbell et al., 2018; Ulrich et al., 2022). Thus, functional imbalance may drive variation in the relative importance of different components of biodiversity effects, providing important context for understanding cases where selection and complementarity show opposite responses (e.g., across resource gradients: He et al., 2024; trait variation: Cadotte, 2017; time: Fargione et al., 2007; invasion: Kuebbing et al., 2015). In such cases, our three components may better identify the conditions maximizing total function: for example, in our simulation of a process shifting the fitness ratio (Figure 4b), additive partition components identify a changing balance between complementarity and selection, but not the optimal fitness ratio optimizing total function predicted by functional coexistence theory ($f_1/f_2=\sqrt{K_1/K_2}$: vertical dashed line in Figure 4b). Thus, we stress that functional coexistence theory and the additive partition provide compatible yet complementary insights into the drivers of ecosystem function.

Identifying mechanisms linking biodiversity and ecosystem function

Beyond these quantitative connections, we highlight how our new functional coexistence framework could complement existing research in identifying the mechanisms responsible for ecosystem function. This has remained a perennial call to action over more than two decades of biodiversity–ecosystem function research (Barry, Mommer, et al., 2019; Hooper et al., 2005; Loreau et al., 2012; Wang et al., 2024) for two reasons. First, knowing the basic biological processes responsible for observed diversity–function relationships could better predict their *context dependence*. Indeed, though experimental evidence (Chen et al., 2025; Zheng et al., 2024) suggests that biodiversity effects are often persistent and positive, these results vary by the system (Chen et al., 2025; O'Connor et al., 2017) and ecosystem function under consideration (Meyer et al., 2016); furthermore, their magnitude and drivers may change over time (Reich et al., 2012; Zheng et al., 2024) and under different environmental conditions (Allan et al., 2011; Furey & Tilman, 2021; Thakur et al., 2021). Second, mechanistic knowledge could help address the *interplay between community and ecosystem dynamics*, which is a crucial difference between experimental and real-world systems (Jiang et al., 2009; Lepš, 2004; Wardle, 2016). For instance, species vary in their sensitivity to global change, and loss of the most sensitive species might have nonrepresentative effects on ecosystem function (Jochum et al., 2020; Zavaleta & Hulvey, 2004). Moreover, relationships between diversity and function may be very different under natural community assembly (Veen et al., 2018), leading to complex feedbacks between species loss and overall ecosystem function (Isbell et al., 2013; Suding et al., 2005). While it is generally agreed that neither the modern coexistence theory components nor the additive partition effects constitute mechanisms in a low-level (e.g., physiological, biochemical, or developmental) sense (Carroll et al., 2012; Loreau et al., 2012; Song et al., 2019), these frameworks have played an indispensable role in linking higher and lower level views of community and ecosystem dynamics (Cadotte, 2017; Kraft et al., 2015; Wang et al., 2024). Indeed, what constitutes a "mechanism" is a matter of perspective—one working definition highlights the ability to explicitly represent "component parts and their associated actions and interactions" (Connolly et al., 2017). Reflecting the divergent aims of their respective fields (Wagg et al., 2019), coexistence theory describes dynamic properties of populations, while the additive partition focuses on abundance at a defined point in time (Box 1, items 1 and 2). Thus, the competitive or facilitative interactions considered under theories of coexistence, which focus on dynamic properties such as growth rates (Chesson, 2000) or feedbacks (Ke & Letten, 2018), do not directly correspond to the abundance effects considered under the additive partition (Wagg et al., 2019), and both do not necessarily exactly relate to underlying biological processes such as resource use (Abrams & Abrams, 2022). As such, functional coexistence theory represents an intermediate level of mechanistic detail: it explicitly considers the population dynamics and species interactions that give rise to community-level coexistence and ecosystem-scale functioning. While such an approach requires more data, it also has the potential (1) to address the *context dependence* of functional outcomes by predicting long-term dynamic outcomes, and (2) to

BOX 4 Applying functional coexistence theory to a consumer–resource model

Here, we use a resource competition model as a case study to show how functional coexistence theory can be applied to more mechanistic models. This Box summarizes the general derivations (given in full in Appendix S1: Section S5) for mathematically interested readers, while the main text provides a verbal overview and specific graphical analyses.

We generalize a one-resource competition model from Tilman (1982) to an arbitrary number of species. We consider n species, each with biomass N_i, and a resource R (Figure 5a). Assuming that R is the single primary limiting factor in the system, we then allow species to interfere with each other's resource uptake in order to implicitly capture the effect of additional limiting factors. The dynamics of the general model are given by the following equations:

$$\frac{dN_i}{dt} = N_i[\varepsilon_i u_i(R, N_1, ..., N_n) - m_i(N_1, ..., N_n)]. \tag{12}$$

$$\frac{dR}{dt} = g(R) - \sum_{i=1}^{n} N_i u_i(R, N_1, ..., N_n) + \sum_{i=1}^{n} \varphi_i N_i m_i(N_1, ..., N_n). \tag{13}$$

Here, a species' growth depends on its resource-use efficiency ε_i and its per capita resource uptake u_i (a function of the abundance of the resource and of other species), and it experiences mortality according to some function m_i. Resource dynamics are governed by some resource supply function g, uptake by consumers, and return from dead biomass, where φ_i is the resource returned per unit of species i's dead biomass.

Linking the model to functional coexistence theory: To link our consumer–resource model to the general results above, we analyze a specific version of the model where species i's resource uptake is reduced by interference: $u_i = v_i R / \left(1 + \sum_{j=1}^{n} \beta_{ij} N_j\right)$, where v_i is i's intrinsic uptake ability and β_{ij} is the strength of resource uptake interference by species j on species i; note that response to interference follows a functional form identical to that of competition in the Beverton–Holt model (Beverton & Holt, 1957). Assuming constant species mortality (i.e., m_i independent of $N_1,...,N_n$) and a closed system ($g(R) = 0$) with complete resource return ($\varphi_i = \varepsilon_i^{-1}$), the total amount of resource in the system (i.e., in R and biomass) is constant and we can derive population dynamics as:

$$\frac{dN_i}{dt} = N_i \left[\frac{\varepsilon_i v_i \left(R_0 - \sum_{j=1}^{n} \varepsilon_j^{-1} N_j \right)}{1 + \sum_{j=1}^{n} \beta_{ij} N_j} - m_i \right], \tag{14}$$

where the conserved quantity $R_0 \equiv R + \sum_i \varepsilon_i^{-1} N_i$ is the total amount of resource in the system (i.e., in the R pool or in biomass); we give the derivation in detail in Appendix S1: Section S5 and show that it can also be interpreted as a first-order approximation to more complex resource dynamics. Since this form corresponds to the class of models considered in Box 2 and Appendix S1: Section S1, we can derive the quantities necessary to apply functional coexistence theory (see full derivations in Appendix S1: Section S5). Namely, we show that the coexistence components are

$$\rho = \sqrt{\frac{b_{12} b_{21}}{b_{11} b_{22}}} \text{ and} \tag{15}$$

$$\frac{f_1}{f_2} = \frac{R_0 - R_1^*}{R_0 - R_2^*} \sqrt{\frac{b_{21} b_{22}}{b_{12} b_{11}}}, \tag{16}$$

where $R_i^* \equiv m_i/(\varepsilon_i \nu_i)$ directly corresponds to Tilman's (1982) R^*, the minimum resource concentration at which species i can maintain positive population growth, and $b_{ij} \equiv \varepsilon_j^{-1} + R_i^* \beta_{ij}$ measures the competitive effect of species j on i via resource uptake and interference. On the other hand, intrinsic yield is

$$K_i = \frac{R_0 - R_i^*}{b_{ii}}. \tag{17}$$

Note that b_{ij} is independent of total resource level, and thus a species' actual sensitivity to competition (sensu Box 2) further depends on total resource level (Appendix S1: Section S5). As a result, monoculture yield is proportional to $R_0 - R_i^*$, the *portion of the resource pool available to species* i, and similarly, fitness ratio (Equation 16) depends on the ratio of resources available to the two species.

Conditions for transgressive overyielding: Applying Equation (7), we straightforwardly find that transgressive overyielding requires

$$\frac{f_1}{f_2} > \frac{R_0 - R_1^*}{R_0 - R_2^*} \cdot \frac{b_{22}}{b_{11}} \cdot \rho, \tag{18}$$

where both the left-hand (fitness ratio; Equation 16) and right-hand sides depend on resource level R_0 only through the ratio of available resource $\left(R_0 - R_1^*\right)/\left(R_0 - R_2^*\right)$. Thus, varying resource level can never change whether this inequality holds. Put simply, because changing resource level affects fitness and function in the same way, it can never change the fitness–function relationship, and thus cannot affect the potential for transgressive overyielding.

account for the *interplay between community and ecosystem dynamics* by identifying low-level mechanistic tradeoffs responsible for both. As such, we expect that our functional coexistence theory framework can pinpoint fundamental connections between community and ecosystem dynamics, particularly when combined with models (Wan & Crowther, 2022) or experiments (Barry, de Kroon, et al., 2019) that address lower level mechanisms.

APPLYING FUNCTIONAL COEXISTENCE THEORY TO THEORETICAL AND EMPIRICAL SYSTEMS

We demonstrate how functional coexistence theory can generate new insights into the mechanistic drivers of ecosystem function using three detailed case studies. First, using a general resource competition model (*Case study 1: Applying functional coexistence theory to a consumer–resource model*), we demonstrate that the theory also applies to multispecies communities and, more importantly, show how it can predict the response of ecosystem function to environmental contexts such as gradients of resource availability. Next, we confirm our predictions using data from a classic plant competition experiment (*Case study 2: Explaining coexistence and productivity in a classic plant competition experiment*), illustrating how functional coexistence theory identifies key tradeoffs driving ecosystem function. Finally, we theoretically extend the framework to multiple ecosystem functions (*Case study 3: linking coexistence and ecosystem multifunctionality*), highlighting that niche difference drives multifunctionality by allowing the community to overcome species-level tradeoffs between functions.

Case study 1: Applying functional coexistence theory to a consumer–resource model

We have introduced functional coexistence theory with the classic Lotka–Volterra model, which only treats species dynamics phenomenologically—that is, it does not represent the biological processes through which species interact with each other and with the environment. In this case study, we show that our framework can be combined with mechanistic models to address links between community and ecosystem properties and predict the context dependence of biodiversity effects. By capturing the context-dependent and interrelated nature of the coexistence components, these mechanistic analyses can

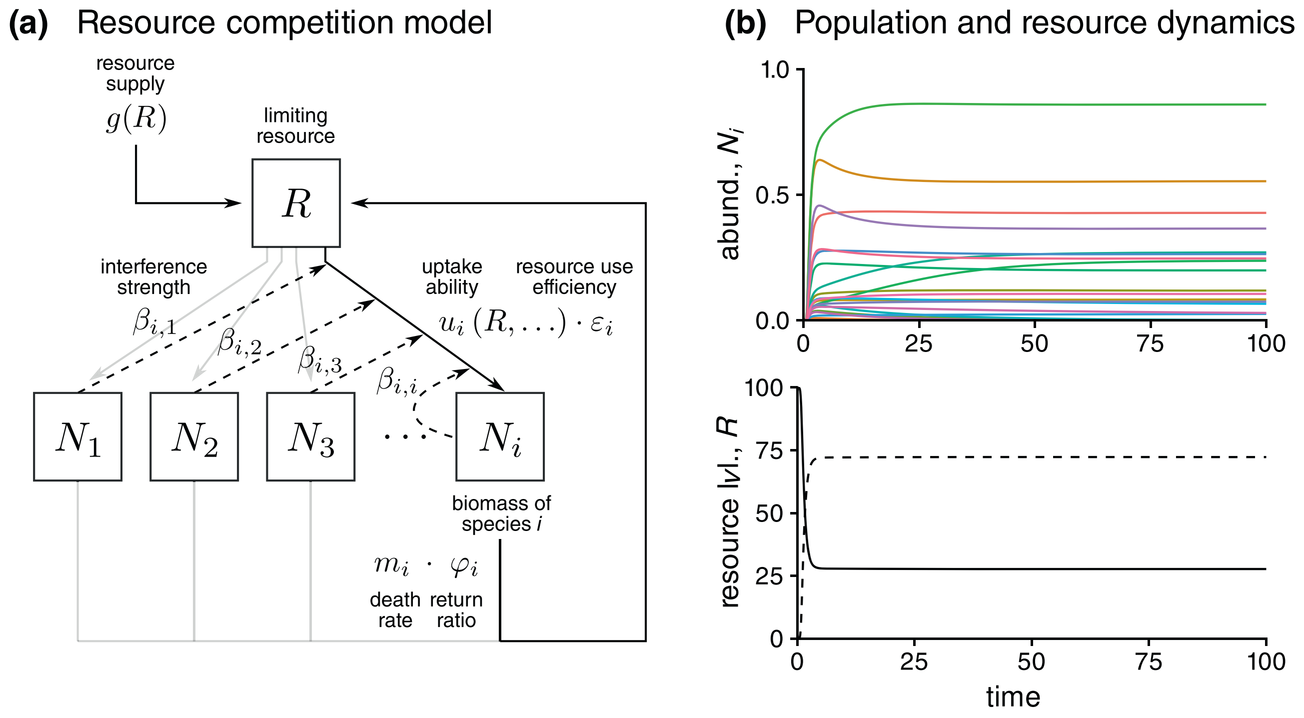


FIGURE 5 (a) Consumer–resource model with interference. A single limiting resource R is taken up by species $N_1, N_2, N_3, \ldots, N_i$ differing in their uptake ability ν_i and resource-use efficiency ε_i, while species-specific mortality m_i returns resources to the pool. Furthermore, species interfere with each other, reducing their ability to take up resources according to interference strength β_{ij}, which captures limitation by factors not explicitly represented in the model. (b) Population and resource dynamics. We show the time series of species abundances N_i (top) and resource dynamics (bottom) for $n = 20$ species. We show the free resource pool R (solid black line) and the total amount of resource contained in consumer biomass (dashed line), such that the total resource level R_0 is conserved. Parameters match the reference multispecies model used in Figure 6 and are described in Appendix S1: Section S8.

address a key limitation of phenomenological models and the modern coexistence framework (Barabás et al., 2018; Song et al., 2019). In particular, we use the consumer–resource framework (Chase & Leibold, 2003; Tilman, 1982): from an ecosystem perspective, these models reflect fundamental constraints on nutrient cycling, resulting in more realistic predictions of resource dynamics (Gross, 2008); from a community perspective, they can succinctly capture species interactions using a minimum of measurements or parameters (Letten & Stouffer, 2019).

A general model of resource competition with interference

We begin by defining a general trait-based resource competition model and calculating our niche, fitness, and function measures, as shown in mathematical detail in Box 4. Closely related to previous models of interference competition (Amarasekare, 2002) and facilitation (Gross, 2008), our model considers the dynamics of an arbitrary number of species N_i competing for a single shared limiting resource R (Figure 5a). Species differ in their ability ν_i to obtain this resource, their resource-use efficiency ε_i, and in their mortality m_i, creating a competitive hierarchy in resource competition. Furthermore, species interfere with the resource uptake of conspecific and heterospecifics (β_{ii}, β_{ij}). Although the number of distinct resources limits the number of coexisting species in models of pure resource competition, this interference term allows an arbitrary number of species to coexist in the present model (Figure 5b; Appendix S1: Figure S4). That is, the limiting factors necessary for coexistence in this model consist of the shared resource R, which is modeled mechanistically, and additional species interactions β_{ij}, which are modeled more phenomenologically. We suggest that this may be an appropriate mechanistic model for systems where species interact in diverse ways, but overall, interactions are strongly structured by competition for a single shared resource. For instance, in a plant system, R could represent space (e.g., in a forest ecosystem: Yuan & Chesson, 2015) or a limiting soil nutrient (e.g., nitrogen: Clark et al., 2018), while β_{ij} could represent more specific factors such allelopathy or shared pathogens (Ke &

Wan, 2020) that affect plants' ability to compete for the shared resource.

Functional coexistence theory relates low-level mechanisms to community- and ecosystem-level consequences

In Box 4, we calculate the niche, fitness, and function components and transgressive overyielding condition for the resource competition model. Functional coexistence theory summarizes the many low-level traits in the model into a few higher level components with clear ecological interpretations. R_i^* measures species i's ability to compete for resources (independently from interference), a critical trait for ecosystem functioning (Tilman, 1982). In turn, we find that fitness ratio and monoculture yield vary with resource level, but the niche component remains constant (Box 4, Equations 15–17). This matches recent empirical findings showing that nutrient addition prevents coexistence in grassland communities through fitness shifts (Dostál, 2023). Therefore, our theory clarifies the effect of mechanistic traits at higher levels of biological organization, a point we further explore below with analyses of multispecies competition and the effect of changing resource levels.

Fundamentally linking community structure and function in multispecies communities

First, we used simulations of the model to determine if functional coexistence theory could predict the *interplay between community and ecosystem dynamics* in a complex multispecies community. This is a crucial test of our theory because a major challenge in biodiversity–ecosystem function research is understanding whether the mechanisms identified in experiments should generalize to the complex feedbacks that emerge when diversity changes and functional outcomes emerge from the same global change drivers (Wardle, 2016). In brief, we randomly drew $n = 20$ species from community-wide distributions of resource competition and interference traits. We then varied the interference terms β_{ij} or β_{ii} to modify the median stabilizing niche differences, fitness–function relationship, or functional imbalance separately between species pairs in the community (see full methods and results in Appendix S1: Section S8). We found that the total biomass of the community changed predictably with these manipulations, consistent with the outcomes in our previous two-species systems (Figure 6). Transgressive overyielding of the community (green shading) required niche differences in excess of the requirements for coexistence (Figure 6a; more clearly visualized in Appendix S1: Figure S9). Moreover, biomass was maximized at a median fitness ratio close to the pairwise optimal value predicted using yield imbalance for species pairs (Figure 6b; dashed vertical line) and reducing functional imbalance always increased total biomass (Figure 6c). These results indicate agreement between the conditions for pairwise and multispecies transgressive overyielding (Appendix S1: Figure S10) The consumer–resource model also captured fundamental relationships between community structure and ecosystem function: communities with more species and more even species abundances (inset rank–abundance curves in each panel) almost always had higher total biomass, consistent with recent work highlighting the role of species evenness in ecosystem functioning (Hordijk et al., 2023). The only exception was one community with a negative tradeoff between fitness and function (Figure 6b, leftmost point and inset rank–abundance curve), consistent with the "function–dominance" hypothesis of Crawford et al. (2021). Thus, our findings highlight that understanding underlying tradeoffs can enhance the prediction of biodiversity effects in species-rich systems (Clark et al., 2018).

Predicting the response of biodiversity effects to resource availability

Most importantly, our analysis of the resource competition model provides insights into how biodiversity effects should depend on resource availability. Nutrient addition and biodiversity loss are important and linked global change drivers (Harpole & Tilman, 2007; Reich et al., 2001), yet understanding their combined effect is particularly challenging because resource availability has consequences at three interacting levels: species-level performance (Wedin & Tilman, 1993), the maintenance of diversity within communities (Dostál, 2023; Harpole et al., 2016), and total functioning at the ecosystem scale (Isbell et al., 2013; Reich et al., 2001). Despite expectations that biodiversity effects may decline under high resource availability due to reduced niche partitioning (Grime, 1977; Wardle, 2016), experimental evidence for this prediction is weak (Craven et al., 2016), with many systems instead showing stronger biodiversity effects under increasing resource levels (Boyer et al., 2009; Fridley, 2002; Godoy et al., 2020; Reich et al., 2001). Our general theoretical findings suggest one possible explanation for the limited and variable effects of nutrient addition reported in meta-analyses of biodiversity experiments (Craven et al., 2016; He et al., 2024; Hong et al., 2022). Using functional coexistence theory, we derive the general condition for transgressive overyielding in the resource competition model (Box 4; Equation 18). Surprisingly, changing resource levels never affects the conditions for transgressive overyielding. We illustrate this counterintuitive finding using numerical simulations (Figure 7a). Increasing resource level (x-axis) increases the fitness advantage of the more productive species (solid line), eventually allowing it to coexist with its competitor (gray region). Yet it also increases the imbalance in monoculture yields, increasing the minimum fitness ratio required for transgressive overyielding (green region). This general result (Equation 18) occurs because resource availability has an identical effect on the fitness and function imbalance between species. In other words, changing resource availability itself while all else is kept equal cannot change the fitness–function relationship, which instead depends on the underlying resource use and interference traits (Appendix S1: Section S5). This highlights the importance of understanding tradeoffs that emerge due to lower level mechanisms: while analysis at a single resource level would suggest that there is high potential for transgressive overyielding at some conditions (Figure 7b, resource level 1), the interdependence of niche, fitness, and function components (Song et al., 2019) caused by resource competition renders transgressive overyielding impossible. More generally, because transgressive overyielding is a special case of other metrics (e.g., ΔY), our result provides an upper bound on biodiversity effects over resource gradients. When interactions are highly structured by single nutrients, we expect shifts in biodiversity effects to be limited in magnitude because they are primarily driven by changes in species coexistence (i.e., fitness f_i/f_j alone), rather than the changes in the fitness–function relationship (i.e., the relationship between f_i/f_j and K_i/K_j) which would maximize functioning. This also provides context for the variability of empirical results: the theoretical expectation is that changes in biodiversity effects in response to resource availability depend on how specific competitive hierarchies (fitness differences) respond to resource availability, rather than on whether resource availability has a consistent effect on niche differences or functional tradeoffs.

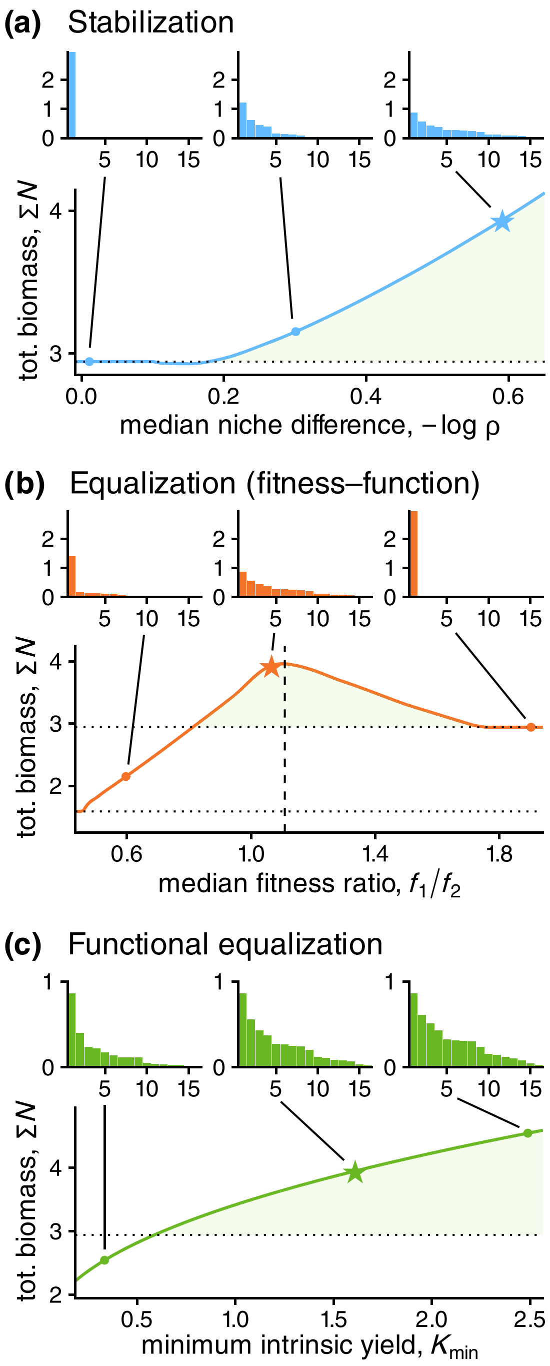


FIGURE 6 Functional coexistence components in multispecies communities. Our analysis parallels Figure 2. We consider a multispecies community ($n = 20$) under the mechanistic resource competition model in Box 4, with traits randomly drawn from statistical distributions (details in Appendix S1: Section S8). Starting from this reference community, we vary the interference terms β_{ij} in order to manipulate (a) stabilization, that is, the median pairwise niche difference, (b) fitness–function relationship, that is, the median pairwise fitness ratio for a higher yielding species versus its competitor, or (c) functional equalization, that is, the minimum monoculture yield. Each main panel shows the total biomass of the community as the strength of the component is varied; the green region highlights transgressive overyielding (relative to the highest-yielding monoculture, indicated with a dotted line). For each scenario, we show the community's rank abundance curve (i.e., plotting species rank on the horizontal axis against abundance on the vertical axis) for three representative points. We indicate the reference community, which is the same in all three panels, with a star.

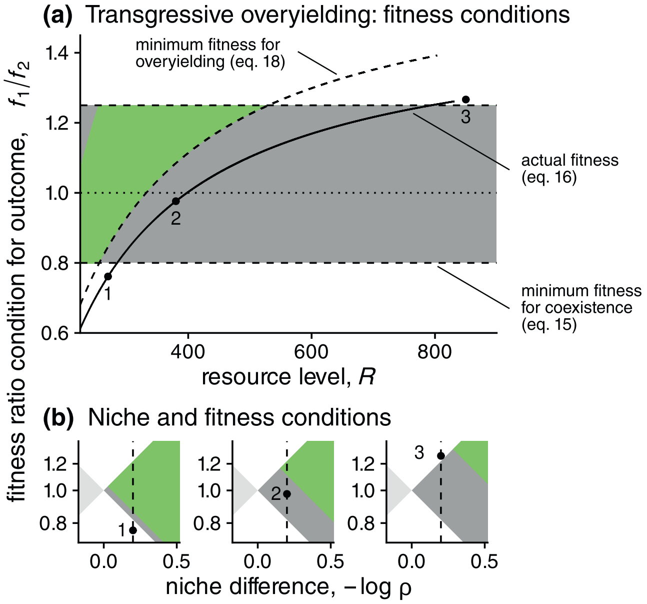


FIGURE 7 Model prediction: Changing resource level alone cannot drive overyielding. For representative parameter values (Appendix S1: Section S8), we show in the top panel how changing resource level affects fitness (solid line). In order to link this to coexistence outcomes, we shade the ratios at which coexistence (gray) and transgressive overyielding (green) could occur at each resource level. The minimum fitness ratio at which overyielding is possible (dashed curve) increases as resource level increases, while the conditions for coexistence (dashed horizontal lines) do not change. Regardless of resource level, the actual fitness ratio is never sufficiently high to allow overyielding due to its mechanistic link to imbalance in monoculture yield. In the lower panels, we show how the communities at resource levels indicated 1–3 in the top diagram can be visualized in the niche and fitness space of Figure 1: Points represent the actual niche and fitness difference, and the green region represents the changing requirements for overyielding.

Case study 2: Explaining coexistence and productivity in a classic plant competition experiment

In order to demonstrate how functional coexistence theory can help integrate theory and experiment, we test the theoretical predictions of our resource competition model by fitting our resource competition model to biomass data from an experiment quantifying plant competition across a soil nitrogen gradient (Figure 8). Working in an extensively studied grassland system (Cedar Creek, Minnesota, USA), the classic study of Wedin and Tilman (1993) competed four pairs of grass species while experimentally manipulating soil nitrogen, the nutrient shown to limit productivity in this system. We selected this study because it directly manipulated limiting resources (corresponding to R_0 in our model); furthermore, extensive mechanistic data collected by the authors alongside their competition experiment provide an opportunity to validate our biological inferences. We applied the functional coexistence framework to investigate overyielding between the only species pair that showed robust coexistence: the grasses *Poa pratensis* and *Agropyron repens*. Using measurements of the species' biomass production in monocultures, we first parameterized each species' R^* and the resource–independent intraspecific interaction parameter b_{ii}; next, since detailed time series data were not available, we fit the resource-independent interspecific interaction parameter b_{ij} to biomass in competition treatments. We then used the fitted parameters to quantify transgressive overyielding and the niche, fitness, and function measures (Figure 8; full methods and parameter fits in Appendix S1: Section S6).

Resource model captures yield and competitive outcomes

The model provided a close fit to monoculture yields, showing that *Poa* had a higher yield than *Agropyron* (Figure 8a, dashed lines; Appendix S1: Figure S5), and that increasing nitrogen availability amplified this difference; however, species differed little in R^* (Appendix S1: Table S3). Model fits successfully predicted changes in competition biomass along the nitrogen gradient (Figure 8a, solid lines), though we found evidence that *Poa*'s sensitivity to competition from *Agropyron* ($\alpha_{Poa,Agr.}$) intensified with increasing nitrogen (Appendix S1: Figure S6), a departure from the theoretical derivation in Box 4. Following observed shifts in biomass with increasing nitrogen, our model predicts a shift from competitive exclusion by *Agropyron* to coexistence with increasing dominance by *Poa*. However, this competitive shift toward the higher yielding species did not result in transgressive overyielding at any nitrogen level (Figure 8b), and the community outperformed average yield only at a relatively small range of high nitrogen values (Appendix S1: Figure S7).

Explaining lack of overyielding using functional coexistence theory

We explain this finding using the functional coexistence components in Figure 8c, which visualizes the fitness ratios enabling coexistence (gray) and transgressive overyielding (green) across the nitrogen gradient. The competitive shift was explained by an equalizing effect of resource availability: higher soil nitrogen increased the fitness ratio in favor of *Poa* (Figure 8c, solid line). While stabilizing niche differences would have been sufficient for transgressive overyielding at low nitrogen (green region; ca. <700 mg/kg), the fitness–function relationship was far from optimal: the higher yielding *Poa* was competitively inferior under these conditions (solid line, where most $f_{\text{Poa}}/f_{\text{Agr.}} < 1$). Although increasing nitrogen favored *Poa*, it simultaneously amplified imbalance in the species' monoculture yields (Figure 8a, dashed lines), thus decreasing the potential for overyielding (vertical range of the green region). This closely corresponds to the predictions by our theoretical analysis (as simulated in Figure 7b): varying soil nitrogen did not change the relationship between the actual fitness ratio and the transgressive overyielding boundary (solid and dashed curved lines). As we showed theoretically in the previous case study, this occurs because resource level has identical effects on fitness ratio and yield ratio. In other words, because function and fitness have the same mechanistic dependence on resource level, changing soil nitrogen level cannot provide the missing fitness–function relationship for transgressive yielding. We therefore conclude that at Cedar Creek, increasing soil nitrogen can change the outcome of competition, but *Poa* always lacks the excess niche difference and fitness advantage that would have allowed transgressive overyielding when it competes with *Agropyron*.

Relating the functional coexistence theory picture to natural history

Complementing the insights available from other methodologies (e.g., selection and complementarity: Appendix S1: Figure S7), our functional coexistence analysis clarifies how competitive processes underpin the lack of transgressive overyielding in this system. Indeed, the mechanistic measurements from Wedin and Tilman (1993) indicated high similarity between *Poa* and *Agropyron*, both in terms of R^* (independently estimated by measuring ability to draw down soil nitrogen) and in resource-use traits, providing ecological context for our finding that the system lacked the excess niche difference required for transgressive overyielding. Furthermore, though the dataset did not allow us to directly fit all

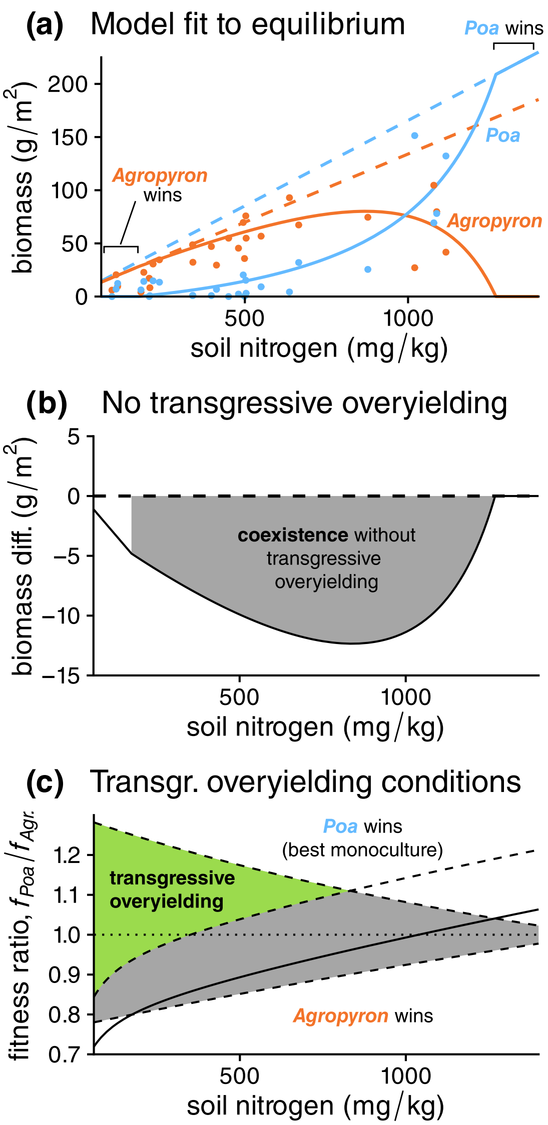


FIGURE 8 Applying functional coexistence theory to a plant competition experiment. We parameterize our resource competition model and identify drivers of pairwise community biomass using experimental data: Wedin and Tilman (1993) competed two grass species, *Poa pratensis* and *Agropyron repens*, across a soil nitrogen gradient (horizontal axis, all panels). Detailed methods are given in Appendix S1: Section S6. (a) Fitting the resource competition model. After determining R^* and monoculture biomass of *Poa* (blue dashed line) and *Agropyron* (orange dashed line) from single-species growth, we fit our model to the plot-level equilibrium biomass of each species (points) across the soil nitrogen gradient. Model predictions (solid lines) capture the shift between *Agropyron* and *Poa* as nitrogen increases. (b) Competitive effect on yield. Using the fitted parameters, we quantified transgressive overyielding (black line) as the difference between the community's biomass and that of its highest-yielding species (*Poa*); we shade the portion of this curve where the outcome was coexistence without transgressive overyielding (gray). (c) Niche and fitness components. We show the predictions of functional coexistence theory for this system, calculating the range of fitness ratios (vertical axis) that would allow transgressive overyielding (green) or just coexistence (gray) across the nitrogen gradient. The solid line shows the actual fitness ratio between the species; the dashed lines show the three boundaries as in Figure 7b.

underlying resource-use parameters, the authors' independent finding that the species had a similar ability to draw down soil nitrogen corroborates our model's R^* fits. This suggests that differences in intrinsic yield may have been driven by *Poa* experiencing less self-limitation from other factors (corresponding to lower $\beta_{Poa,Poa}$), or by it producing more biomass from available nitrogen (higher ε_{Poa}), both of which prevent transgressive overyielding by promoting a negative tradeoff between fitness and function (Appendix S1: Equation S87). Indeed, our model fits indicate that despite its higher monoculture biomass, *Poa* was much more sensitive to competition from heterospecifics than *Agropyron* across the entire nitrogen gradient (Appendix S1: Figure S6). Thus, we highlight that, in tandem with manipulative experiments, our functional coexistence approach can identify the biological mechanisms responsible for changes in community function.

Case study 3: Linking coexistence and ecosystem multifunctionality

Though our derivations and examples focus on processes promoting biomass production, we stress that the results of functional coexistence theory can apply to any ecosystem function (e.g., nutrient cycling: Godoy et al., 2020 or other ecosystem services: Hooper et al., 2005), as we prove in Appendix S1: Section S7. Moreover, going beyond previous approaches, functional coexistence theory can consider these functions simultaneously, allowing it to address an emerging synthesis considering biodiversity's effect on *multifunctionality*, the ability for ecosystems to maintain multiple processes or services (Hector & Bagchi, 2007). Our framework represents a more mechanistic way of considering ecosystem multifunctionality because it captures the individual populations responsible for particular functions, and how these interact. Accordingly, we apply functional coexistence theory to study the conditions allowing ecosystems to show transgressive overyielding for more than one function.

Generalizing functional coexistence theory to function

To generalize our framework, we begin by noting that Equation (4), which describes species' biomass contributions to the community, can be multiplied by function per unit biomass at equilibrium φ_i to obtain species' functional contributions. This means the quantitative results of the framework can be extended to other functions simply by considering $\Phi_i = K_i \cdot \varphi_i$ instead of K_i. Under the further assumption that function per unit biomass is constant, Φ_i is simply a species' monoculture yield *in terms of function*, instead of *biomass* yield. While this interpretation may not hold for all systems (Dee et al., 2019), it is likely realistic for many functions such as enzyme-mediated biogeochemical processes (Dick, 2011), and in more complex cases, it can serve as a starting point for further addressing nonlinearity (e.g., Baert et al., 2017). With this extension, we can now consider conditions for simultaneous overyielding. In Figure 9, we add a second function (e.g., litter decomposition) to our previous simulations (Figures 1 and 2) and consider the conditions promoting transgressive overyielding for both functions. As the parameters for this simulation are shared with those for previous analyses (e.g., Figures 1–4), function 1 here corresponds to biomass production. In particular, we consider the case where the species follow a tradeoff between the two functions: in isolation, species 1 produces more function 1 (i.e., biomass) but species 2 has a higher level of the other function (i.e., $K_1/K_2 > 1$, but $\Phi_1/\Phi_2 < 1$). Accordingly, each function is maximized at a different fitness ratio (Figure 9a). Nonetheless, niche and fitness measures remain important for predicting multifunctionality: though Figure 9b shows that lower niche difference values ($-\log\rho = 0.16$ to 0.34) only allowed transgressive overyielding for one function that corresponds to the competitively dominant species, higher niche difference ($-\log\rho = 0.45$) allowed simultaneous transgressive overyielding for both functions. Put conceptually, since competitive outcomes favor functions associated with the fitter species, communities may display the same functional tradeoffs as their component species. However, niche differences in excess of those required for coexistence can overcome these tradeoffs, allowing communities to outperform individual species across multiple functions.

Multifunctionality through the lens of coexistence theory

Though it has been suggested that communities consisting of species performing different functions should show multifunctionality (Hector & Bagchi, 2007), functional coexistence theory clarifies that this depends on the niche and fitness measures between these species. Without the excess niche and fitness differences that promote biodiversity effects, a community cannot simultaneously exhibit high levels of functions performed by different species. Our more general theoretical analysis (summarized for two functions in Figure 9a) clarifies that outcomes depend on the pair of functions showing the

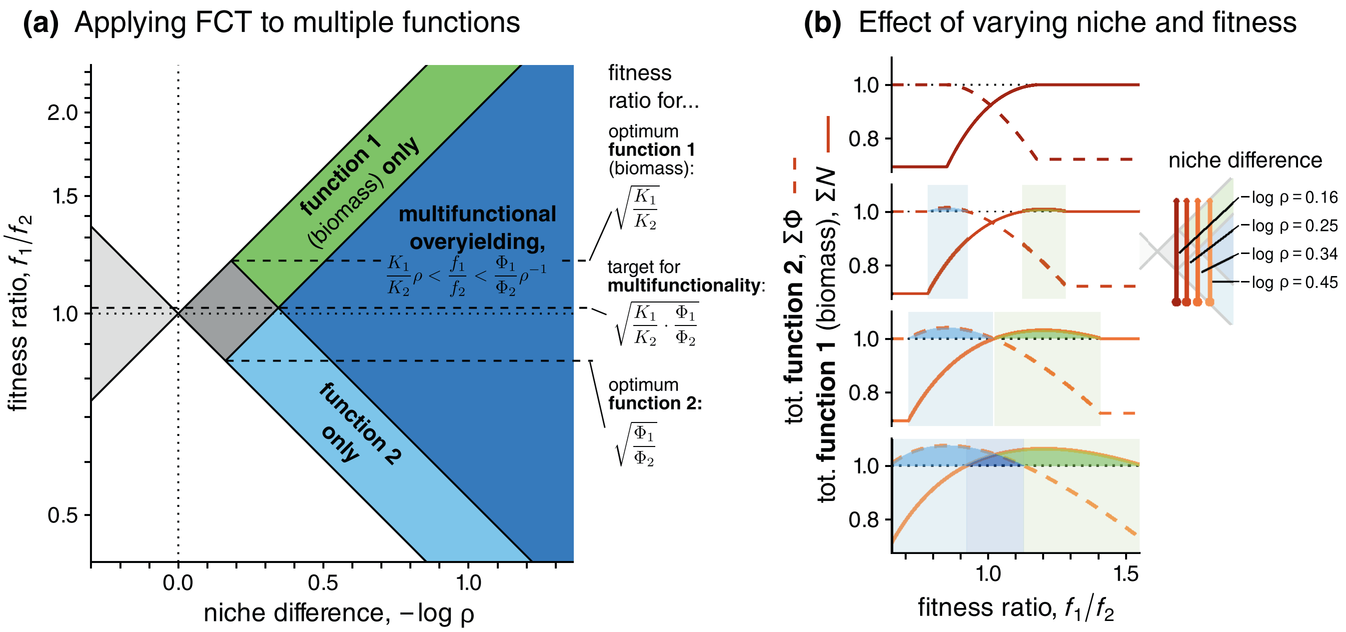


FIGURE 9 Applying the framework to multiple ecosystem functions. Using the same parameter values as in Figures 1 and 2, we also allow the species to differ in a second function where species 2 has a higher monoculture yield ($\Phi_1/\Phi_2 = 0.72/1$), as opposed to biomass (now labeled as function 1) where species 1 has higher intrinsic yield ($K_1/K_2 = 1/0.694$). (a) Applying functional coexistence theory to predict multiple functions. As in Figure 1b, we show niche–fitness combinations where species coexist without showing transgressive overyielding (dark gray region), where the community transgressively overyields only in terms of function 1 (biomass; green), only in terms of function 2 (light blue), and simultaneously for both functions (dark blue). We also indicate the optimal fitness ratio values for each form of overyielding (derived in Appendix S1: Section S1), which represents the fitness ratio value that maximizes the corresponding function. (b) Effect of varying niche difference and fitness ratio. Each subpanel shows the effect of fitness ratio (horizontal axis) on function 1 (biomass; solid line) and function 2 (dashed line) under different values of niche difference, also indicated by line color; the inset shows values of niche difference and trajectories in the niche–fitness space. At lower niche differences, only one form of transgressive overyielding is possible (light blue or green shading), but at the highest niche difference, the community can simultaneously overyield in terms of both functions (dark blue shading). See Appendix S1: Section S8 for parameter values.

strongest tradeoff (i.e., with the most dissimilar yield ratios): the stronger the tradeoff between functions, the more stabilizing niche difference is required for multifunctionality (full analysis given in Appendix S1: Section S7, including more than two functions and outcomes beyond simultaneous transgressive overyielding). More specifically, transgressive overyielding for multiple functions is possible when niche differences provide strong enough stabilization to overcome this dissimilarity, and when the fitness ratio is sufficiently equalized (i.e., close enough to the geometric mean of these two yield ratios). Indeed, in an experimental test of the relationship between coexistence components and multiple ecosystem functions, Godoy et al. (2020) found that high niche difference and similarity in fitness increased both biomass production and litter decomposition rate in diverse plant communities, emphasizing the importance of excess niche difference for multifunctionality. Agreeing with these empirical findings, our results shed light on the general importance of stabilization and equalization for ecosystem function.

CONCLUSION: SYNTHESIZING COMMUNITY AND ECOSYSTEM PERSPECTIVES IN A CHANGING WORLD

By showing fundamental links between modern coexistence theory and ecosystem function, our findings link community and ecosystem processes. We show that a simple condition predicts when coexistence increases the total function of a community: species must experience niche differences and fitness advantages in excess of those required for coexistence. Thus, our theoretical framework, which we term functional coexistence theory, explicitly identifies three processes that explain biodiversity–function relationships: stabilizing niche differences, fitness–function relationships, and functional equalization, which we demonstrate can be applied to mechanistic models or experimental data, and can be extended to multiple species or ecosystem functions. Accordingly, we envision that synthesis between community and ecosystem principles will offer a promising path forward toward a more general and predictive understanding of ecosystem function.

Resolving debates at the interface of coexistence and diversity–function theory

By demonstrating the compatibility of modern coexistence theory with the additive partition, our work adds to a growing shift in both fields from particular metrics to the conceptual processes encoded by these metrics (Clark, Hillebrand, & Harpole, 2019; Godwin et al., 2020; Loreau & Hector, 2019). For instance, recent work has highlighted that, despite apparent quantitative disagreement, different formulae for the components of modern coexistence theory generally encode shared intuition regarding how biological processes affect species' abilities to persist (Barabás et al., 2018; Godwin et al., 2020). Similarly, we found that complementarity measures the same conceptual process as niche difference: reduction in the amount of competition species experience from heterospecifics, quantified using the invasion growth rate (our F_i) as a "common currency" (Box 3; Appendix S1: Section S4; Grainger et al., 2019). Thus, we hope that our work builds a quantitative foundation for studies to compare and ultimately integrate the two approaches (e.g., Godoy et al., 2020). The precise nature of the relationship between modern coexistence theory's metrics and the additive partition's components has been a matter of contentious debate (Carroll et al., 2011; Pillai & Gouhier, 2019), leading to better understanding of each approach's scope (Turnbull et al., 2013; Wagg et al., 2019; Wang et al., 2024) and stimulating the development of useful new methodology (Barabás et al., 2018; Saavedra et al., 2017; Tao et al., 2024; Ulrich et al., 2022). We suggest that the most important question is not whether quantitative differences between metrics indicate that one set is "skewed" (Carroll et al., 2011, 2012; Loreau et al., 2012), nor whether their close relationship indicts biodiversity effects as an "artefact of coexistence" (Loreau & Hector, 2019; Pillai & Gouhier, 2019; Wagg et al., 2019). Rather, if the goal is to understand high-level outcomes—the dynamics of entire ecosystems—in terms of low-level processes—organisms' interactions with each other and their environment—then the approaches are simply different routes to this destination, and we would benefit from understanding their common ground. Functional coexistence theory provides another such route, and synthesizes many of the benefits of each approach, particularly when integrated with models and experiments that directly address biological mechanisms (Eisenhauer et al., 2016).

New methodologies for coexistence and ecosystem function research

The fundamentally different scopes of the modern coexistence and biodiversity–ecosystem function paradigms also offer complementary perspectives for understanding ecosystem function. Coexistence theory aims to understand the equilibrium or long-term attractor of a system of interacting species, while biodiversity–ecosystem function research tends to focus on outcomes over defined time frames in real communities. Though the two approaches are therefore suited to different questions, we expect that investigations within each scope can benefit from new research methodologies and questions informed by the present synthesis. From the perspective of modern coexistence theory, studies applying niche and fitness differences might be able to provide important information on fitness–function tradeoffs (as in our case study using a plant competition experiment), yet not all such studies directly use abundance and performance measures related to ecosystem function (e.g., they may instead measure individual density or seed count). In these cases, experimentalists can consider investing the relatively small amount of effort required to estimate yield in terms of function (e.g., by measuring a few individuals' biomass or nutrient uptake) in order to apply the functional coexistence framework. Theoretically, future work could extend our findings linking biomass at equilibrium to invasion-based fitness and monoculture yield (Equation 4; Appendix S1: Figure S12) to reveal how ecosystem function is affected by fluctuation-dependent coexistence mechanisms (Ellner et al., 2019), nonlinear and higher order interactions (Gibbs et al., 2022), or intransitive competition (Saavedra et al., 2017). Meanwhile, in the realm of biodiversity–ecosystem function studies, some existing datasets from well-replicated and/or long-term biodiversity experiments provide enough information to fit dynamic models (Barbier et al., 2021), and in other systems, simple invasion experiments or observations of natural community reassembly after the end of experiments (Veen et al., 2018) might provide estimates of invasion-based fitness F_i. As recent work has highlighted (Godoy et al., 2020), designing experiments that simultaneously implement approaches from biodiversity–ecosystem function and coexistence theory is a key step forward in validating the connections between community and ecosystem dynamics.

Why coexistence theory?

Our results indicate the niche and fitness components from coexistence theory are compatible with complementarity and selection effects from the biodiversity–ecosystem function literature. As such, if the approaches' results overlap, why bother with the greater effort of implementing coexistence theory? One reason is that it offers a more precise quantitative picture of exactly how different processes interact to determine ecosystem function. One of the key contributions of the niche–fitness framework was clarifying that differences between species can either help or hinder coexistence (Adler et al., 2007). Thus, even extremely detailed information about species' functional capacities may be misleading without quantitative tools to understand their effect on population dynamics (Kraft et al., 2015). Paradoxically, species with high trait similarity may nonetheless coexist if this similarity equalizes fitness differences (e.g., as Narwani et al., 2017 demonstrated for algae with nearly identical gene expression). Similarly, we expect functional coexistence theory to help clarify the complex and counterintuitive effects of functional trait variation on biodiversity–ecosystem function relationships. For instance, though Cadotte (2017) found that functional trait diversity increased biodiversity effects, consistent with its potential role in niche difference–mediated complementarity, other studies have indicated trait-dependent (Flynn et al., 2011) or overtly negative effects of trait diversity (Finegan et al., 2015; Huxley et al., 2023; Liu et al., 2024). Paired with appropriate manipulative experiments, our quantitative perspective could identify precise mechanistic tradeoffs between niche, fitness, and function that promote or hinder ecosystem function. As an example of the benefits of understanding these key tradeoffs, we highlight the recent culmination of decades of work at Cedar Creek on the mechanisms underpinning coexistence (Harpole & Tilman, 2007) and ecosystem function (Hille Ris Lambers et al., 2004), which allowed Clark et al. (2018) to predict the system's entire patterns of species abundances and biodiversity–ecosystem function from a simple tradeoff among three resource-use traits. We point to functional coexistence theory as a tool that could accelerate the identification of such key tradeoffs, unifying the prediction of community and ecosystem dynamics in challenging real-world systems.

The value of theory in the search for mechanism

More broadly, we echo recent suggestions that moving forward in biodiversity–function research requires searching for the shared mechanisms that structure both communities and ecosystems (Hooper et al., 2005; Loreau, 2010; Mayor et al., 2024; Turnbull et al., 2016; Wang et al., 2024). Indeed, carefully designed experiments have already helped to identify ecological first principles responsible for diversity–function relationships (reviewed in, e.g., Barry, de Kroon, et al., 2019), from symbiotic interactions (Eisenhauer et al., 2010; Van der Heijden et al., 1998) and facilitation (Wright et al., 2017) to spatial organization (Noulèkoun et al., 2024; Tatsumi & Loreau, 2023; Williams et al., 2017). Our framework could help enrich this growing consensus by bridging the questions of the biodiversity–ecosystem function literature with the rich theoretical foundations of the modern coexistence theory literature. Indeed, studies in hundreds of systems have quantified niche and fitness differences (Buche et al., 2022) and attributed them to specific biological mechanisms (e.g., Yan et al., 2022), often finding stabilizing and equalizing forces in excess of the requirements of coexistence (Buche et al., 2022; Levine & HilleRisLambers, 2009). Our framework clarifies that these excesses—Adler et al.'s (2010) "embarrassment of niches"—should work to maximize the total functioning of a community. As empirical work increasingly seeks to build predictive understanding by identifying the specific biological mechanisms driving ecosystem function, the modern coexistence theory literature can thus offer a valuable launch point (Godoy et al., 2020; Turnbull et al., 2016; Wang et al., 2024). Accordingly, we emphasize the utility of ecological theory for addressing today's pressing challenges. By integrating established theory from community and ecosystem ecology, we repurpose well-studied tools to provide a fundamental understanding of the relationship between coexistence and ecosystem functioning. Adding to a growing synthesis of ecological theory across scales to address anthropogenic environmental change (Hallett et al., 2023; Mayor et al., 2024), we hope that the functional coexistence framework presented here will help build a more predictive understanding of Earth's ecosystems and their roles in a changing world.

AUTHOR CONTRIBUTIONS

Joe Wan conceived the study with input from Thomas W. Crowther. Joe Wan and Iris Hordijk designed the resource competition model, and Joe Wan and Po-Ju Ke designed the remaining analyses with input from all authors. Joe Wan wrote analysis code and derived the theoretical results. Joe Wan and Po-Ju Ke drafted the manuscript with equal contributions, and all authors contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All code and inputs (Wan, 2025) are available on Zenodo at https://doi.org/10.5281/zenodo.16423509.

ORCID

Joe Wan https://orcid.org/0000-0001-5950-2353
Po-Ju Ke https://orcid.org/0000-0002-8371-7984
Iris Hordijk https://orcid.org/0000-0002-6302-6254
Lalasia Bialic-Murphy https://orcid.org/0000-0001-6046-8316
Thomas W. Crowther https://orcid.org/0000-0001-5674-8913

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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