Resource diversity begets stability in complex ecosystems

Jamila Rowland-Chandler[1], Wenying Shou[1, *], and Akshit Goyal[2, *]

[1]Centre for Life's Origins and Evolution, Department of Genetics, Evolution and Environment, University College London, WC1E 6BT, United Kingdom
[2]International Centre for Theoretical Sciences, Tata Institute of Fundamental Research, Bengaluru 560089, India
[*]Equal contribution corresponding author (order determined by a coin flip).

Electronic addresses: W. Shou: wenying.shou@gmail.com; A. Goyal: akshitg@icts.res.in

Abstract

A fundamental paradox in ecology is the relationship between species diversity and ecosystem stability: while May's stability condition predicts that species diversity destabilises communities, many diverse ecosystems in nature are stable. Here, we resolve this paradox by explicitly modelling the resource dynamics that control species diversity, which May neglects. Although increasing resource diversity can increase species diversity (the competitive exclusion principle) and thus should destabilise communities according to May, we find the opposite: resource diversity consistently generates stable, species-rich communities. Furthermore, we show that contrary to the prevailing belief that interaction heterogeneity is always destabilising, different biological sources of interaction variance have opposing effects on stability. Our analytically derived stability condition showed that, consistent with previous work, stability is always induced when the correlation between growth and consumption exceeds the square root of species packing ratio (the number of surviving species/the number of surviving resources). Our work overturns a longstanding view in theoretical ecology, and demonstrates that resource dynamics are not just negligible background but are central drivers of ecosystem stability.

Introduction

Ecological communities exhibit diverse dynamical behaviours, ranging from perturbation-resistant mono-stable states [1, 2] to multi-stability [3–5] to persistent fluctuations [6–12]. The dynamical behaviour of a community is critical for its functioning. For example, stability —the ability of a community to return to the original steady state after a small perturbation —can preserve the healthy metabolism of gut microbiomes, while pathogen invasion can drive the emergence of low-diversity, fluctuating diseased states [13, 14]. In contrast, fluctuations and turnover of soil communities can promote nutrient cycling [15–17] critical for crop and ecosystem productivity. Given the importance of ecological dynamics, ecologists have sought to understand how they arise from interactions between community members and their resource environment, such as competition for shared resources or cross-feeding [18–21] .

Theoretical ecologists have attempted to understand the mechanisms driving stability and other dynamics using mathematical models. Traditionally, these studies used models where species interact directly (e.g., the generalised Lotka-Volterra model, or gLV), without accounting for the resource dynamics that mediate these interactions [22–27]. These "resource-implicit models" have revealed seemingly universal mechanisms that stabilise or destabilise communities. For example, Robert May and others suggested that species-rich communities with heterogeneous inter-species interactions are inherently unstable — this is known as "May's stability condition" (Fig. 1 B, [8, 25–29] although exceptions exist [22]). However, these theoretical predictions often conflict with empirical evidence. Field studies have demonstrated that species diversity can stabilise dynamics in community biomass [30, 31], species abundances [32, 33], and can increase resilience to perturbations [34]. This discrepancy between theory and observation may occur because resource-implicit models ignore the resource dynamics that mediate many species interactions [18, 21, 35–48]. Thus, it remains unclear whether stability conditions from resource-implicit models will

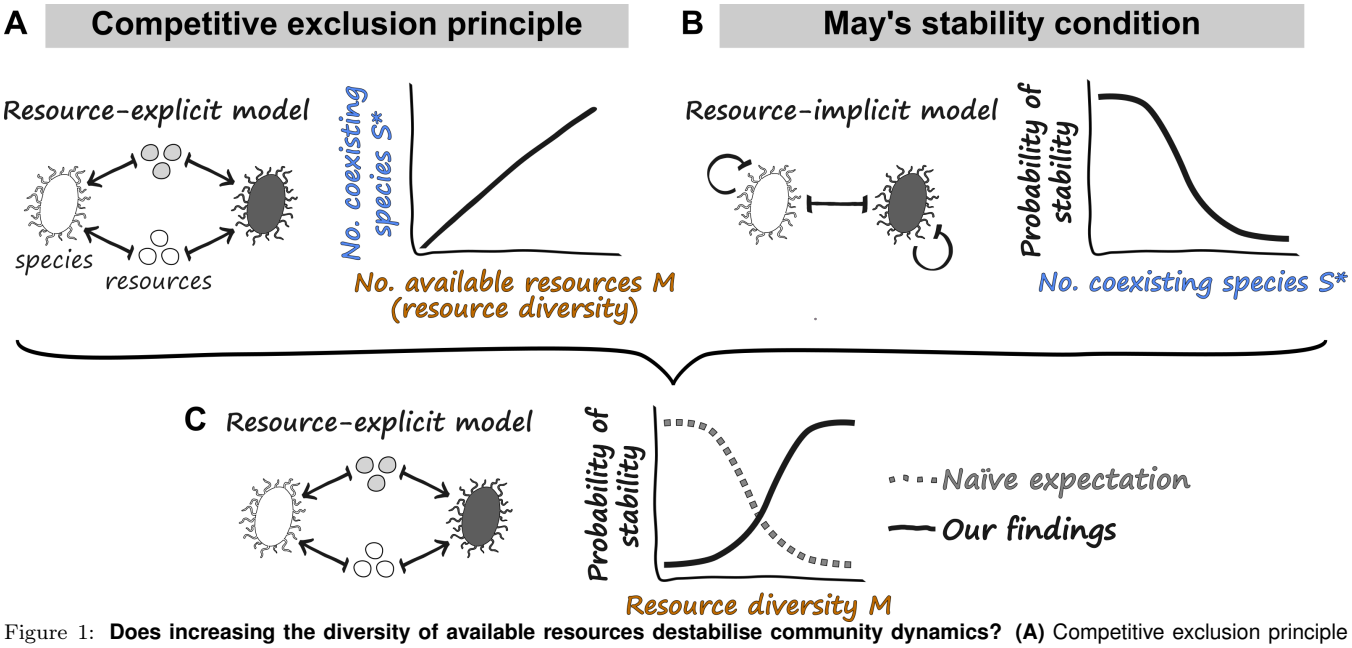

Figure 1: **Does increasing the diversity of available resources destabilise community dynamics? (A)** Competitive exclusion principle (derived from resource-explicit models): Increasing the number of available resources can support more co-existing species. **(B)** May's stability condition (derived from resource-implicit models): Increasing the number of coexisting species should destabilise community dynamics. **(C)** Combining these principles, we naïvely expected that increasing the number of available resources would destabilise community dynamics by increasing species diversity (grey dotted line). However, we found the opposite (black line).

hold when resources are modelled explicitly, or whether resource-explicit models reveal alternative stability relationships that could explain the empirically-observed stabilising effects of species diversity. A critical test case is combining May's stability condition with the foundational competitive exclusion principle, which states that higher resource diversity can support more coexisting species [49–51] (Fig. 1 A). Together, these principles predict that increasing the diversity of resources in the environment should destabilise communities by increasing species diversity (Fig, 1 C). Yet, this hypothesis has not been directly tested.

Here, we tested whether increasing the diversity of available resources, measured by resource pool size (M), destabilises community dynamics (Fig. 1 C) using a resource-explicit consumer-resource model. Contrary to expectations (Fig. 1 C), increasing the resource pool size increased species richness and stabilised community dynamics. Given this surprising result, we also investigated another prevailing belief: that heterogeneity in species interactions always destabilises communities [25–27, 29, 52–55]. Our model couples resource consumption to species growth via a biologically intuitive yield conversion factor, which allowed us to generate interaction heterogeneity through two distinct biological mechanisms: variance in consumption (σ_c^2) or variance in the yield conversion factor (σ_y^2). Again contrary to expectation, different sources of heterogeneity induced opposing stability transitions: high variance in consumption (σ_c^2) stabilised communities, whereas high variance in yield conversion (σ_y^2) destabilised communities.

To understand these phenomena, we analytically derived the model's stability condition, which requires the correlation between growth and consumption coefficients to exceed the square root of the species packing ratio (the ratio between the number of surviving species and the number of surviving resources) [52, 56, 57]. The growth-consumption correlation is a measure of interaction reciprocity ("reciprocity"), since growth reflects the impact of resource on consumer, while consumption reflects the impact of consumer on resource. When the resource pool size M was small, reciprocity was smaller than $\sqrt{\text{packing ratio}}$, making communities unstable. Increasing the resource pool size increased both quantities, but reciprocity grew faster and ultimately exceeded $\sqrt{\text{packing ratio}}$, generating stable and species-rich communities. Increasing variance in consumption σ_c^2 stabilised communities through a similar mechanism. In contrast, increasing variance in yield σ_y^2 reduced reciprocity faster than reducing $\sqrt{\text{packing ratio}}$, leading to instability. Together, our results demonstrate that resource dynamics can fundamentally alter the relationship between ecological diversity, interaction heterogeneity, and stability, and help reconcile theoretical predictions with empirical observations.

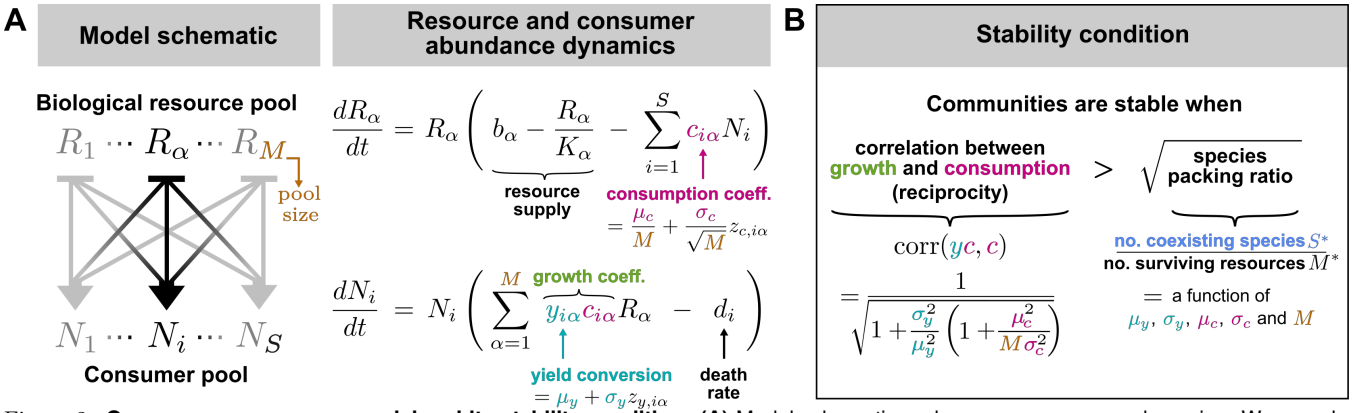

Figure 2: **Our consumer-resource model and its stability condition. (A)** Model schematic and consumer-resource dynamics. We sample yield conversion factors from a normal distribution with mean μ_y and variance σ_y^2. We sample consumption coefficients from a normal distribution with mean μ_c/M and variance of σ_c^2/M, because resources are substitutable and thus high resource diversity leads to less consumption per resource. **(B)** The stability condition, derived using the cavity method. Note that throughout the manuscript, we focus on the effect of changing resource pool size (M) **not** the number of surviving resources (M^*).

The model

In our consumer-resource model, a pool of S consumer species grows by consuming a pool of M resources. The dynamics of resource α (R_α) and consumer i (N_i) are described by the following set of ordinary differential equations:

$$\frac{dR_\alpha}{dt} = R_\alpha \left(b_\alpha - \frac{R_\alpha}{K_\alpha} - \sum_{i=1}^{S} c_{i\alpha} N_i \right), \tag{1}$$

$$\frac{dN_i}{dt} = N_i \left(\sum_{\alpha=1}^{M} y_{i\alpha} c_{i\alpha} R_\alpha - d_i \right). \tag{2}$$

Here, resource (e.g., phytoplankton) grows logistically with b_α being the intrinsic growth rate and K_α being the carrying capacity of resource α (both set to 1 without loss of generality). Consumers (e.g., heterotrophic microbes) deplete resources, where $c_{i\alpha}$ is the "consumption coefficient" of resource α by consumer i (i.e., consumption rate per capita consumer per unit resource). We assumed that all resources are substitutable (e.g., different types of carbon instead of carbon versus nitrogen), so they contribute additively to consumer growth rates (for a full list of assumptions and model details, see SI Appendix B). Consumer species i dies with a death rate of d_i, and grows by converting consumed resources into biomass via $y_{i\alpha}$, which is the yield conversion factor for species i on resource α. The resulting per capita growth rate of species i from consuming resource α is thus given by $y_{i\alpha} c_{i\alpha} R_\alpha$, where we denote $y_{i\alpha} c_{i\alpha}$ as the "growth coefficient" (i.e., per capita growth rate per unit resource). Because yield conversion is consumer-specific, growth and consumption coefficients are *non-reciprocal*, meaning they are not perfectly correlated. This non-reciprocity is crucial for communities to display both stable and unstable dynamics in different parameter regimes [52, 57].

To understand how the resource pool affects the diversity and stability of these complex communities, we followed a long tradition of treating the large number of model parameters as random variables [24, 25, 27–29, 36, 55, 58–64]. Because the total resource consumption rate cannot continue to increase arbitrarily with resource pool size M, we assumed that the consumption coefficient for each resource decreases with resource pool size M ($c_{i\alpha} \propto 1/M$). Thus, we sampled each $c_{i\alpha}$ from a normal distribution with mean μ_c/M and variance σ_c^2/M (Fig. 2 A). We sampled yield conversion factors $y_{i\alpha}$ from a normal distribution with mean μ_y and variance σ_y^2 (Fig. 2 A). For complete details of the model parametrisation and simulations, see SI Appendices B and D. Our central results are robust to many details of parameter choices (e.g., the choice of distribution and values of consumption coefficients and yield conversion factors) as well as some details of the formulation of the model (SI Appendices E and G).

Results

A large resource pool size stabilises species-rich communities

The competitive exclusion principle states that increasing the diversity of available resources can support more species, which, according to May's theory, should destabilise community dynamics (Fig. 1). We tested this hypothesis by simulating community dynamics across different resource pool sizes M (our measure of resource diversity). As expected, larger resource pool sizes supported greater species diversity (Fig. 3 A), but contrary to our prediction, these diverse communities were also more stable (Fig. 3 B and C). Communities with smaller resource pools, in contrast, exhibited persistent fluctuations characteristic of unstable dynamics (Fig. 3 D, compare top and bottom panels). These results demonstrate that resource-explicit dynamics can generate a positive relationship between species diversity and community stability, in stark contrast to the negative relationship identified in resource-implicit models.

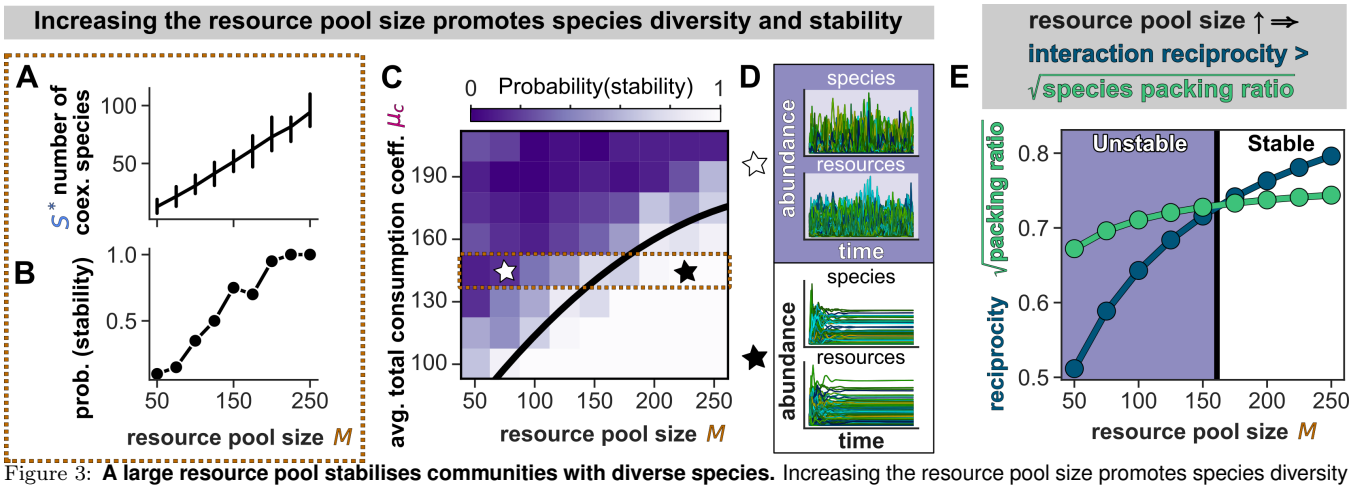

Figure 3: **A large resource pool stabilises communities with diverse species.** Increasing the resource pool size promotes species diversity **(A)** and community stability **(B)**, in direct opposition of our naïve expectation in fig. 1 C. Shown are simulations for $\mu_c = 145$, corresponding to the outlined area in panel (C). **(C)** Stability diagram as a function of resource pool size (M) and average total consumption coefficient μ_c. Each cell shows results from 20 simulated communities, with darker shades indicating a higher proportion of simulations showing unstable, chaotic dynamics (with maximum Lyapunov exponent > 0). Purple: unstable region; white: stable region. The black line shows the analytically-derived stability boundary (SI Appendix C). **(D)** Representative examples of community dynamics from the unstable region with chaotic abundance fluctuations (white star, top) and from the stable region (black star, bottom). Each curve in each plot represents a single species or resource, as labeled. **(E)** Increasing the resource pool size stabilises communities by increasing the interaction reciprocity faster than $\sqrt{\text{packing ratio}}$. Shown are analytically-derived values of the reciprocity (dark blue), $\sqrt{\text{packing ratio}}$ (green) and the stability boundary (black) for $\mu_c = 145$.

Large resource pools stabilise diverse communities by increasing interaction reciprocity faster than $\sqrt{\text{species packing ratio}}$

To understand how resource dynamics can invert the negative diversity-stability relationship predicted by resource-implicit models, we analytically derived our model's stability condition using the cavity method (SI). This is a statistical physics approach that explains how community-level properties arise from ecological interactions [27, 52, 58, 59, 65–67]. Consistent with previous studies in resource-explicit models [52, 56, 57], we found that communities are stable when the correlation between growth and consumption exceeds the square root of the species packing ratio ($\sqrt{\text{packing ratio}}$) (Fig. 2 B).

High reciprocity between growth and consumption (≈ 1) indicates that consumers "efficiently" exploit their metabolic niches [57] as they predominantly consume resources that promote rapid growth and minimally consume resources that do not. The packing ratio — the ratio of surviving species to surviving resources (Fig. 2 B) — quantifies how densely consumers pack into niche space. Due to competitive exclusion, this ratio is generically less than 1, except in "supersaturated" communities with extremely fine-tuned consumption patterns [68, 69]. Therefore, we can interpret the stability condition as the following: reciprocity sets an upper bound on the number of species that can coexist without encroaching on each other's niches ([57], SI Appendix F). For example, high reciprocity means that consumers efficiently exploit distinct niches, enabling them to densely pack into communities without encroaching on

each other's niches; therefore, consumers stably coexist. However, when the $\sqrt{\text{packing ratio}}$ exceeds the reciprocity, consumers continuously encroach on each other's niches, which destabilises community dynamics.

Unlike previous studies, in our model both reciprocity and the species packing ratio emerge naturally from the mechanisms underpinning consumer-resource interactions rather than being imposed *a priori* [52, 56, 57]. This allowed us to determine how both the reciprocity and packing ratio change with resource pool size (Fig. 2 B), as well as how other interaction parameters (e.g. the mean and variance in consumption and the yield coefficients) affect community stability (which we explore later). We found that small resource pools produced unstable communities because in this case, $\sqrt{\text{packing ratio}}$ was much higher than the reciprocity. Increasing the resource pool size raised both reciprocity and $\sqrt{\text{packing ratio}}$, but reciprocity rose much faster, meaning communities eventually became stable (Fig. 3 E, black transition). As we show in Fig. 2 A, the exact transition point is not fixed and instead depends on several factors, such as a consumer's average consumption of all resources (μ_c). However the qualitative picture is robust: increasing the resource pool size generates species-rich and stable communities by increasing reciprocity faster than $\sqrt{\text{packing ratio}}$, which prevents densely-packed consumers from encroaching on each other's niches.

Increasing heterogeneity in consumer-resource interactions through different biological mechanisms induces opposing stability transitions

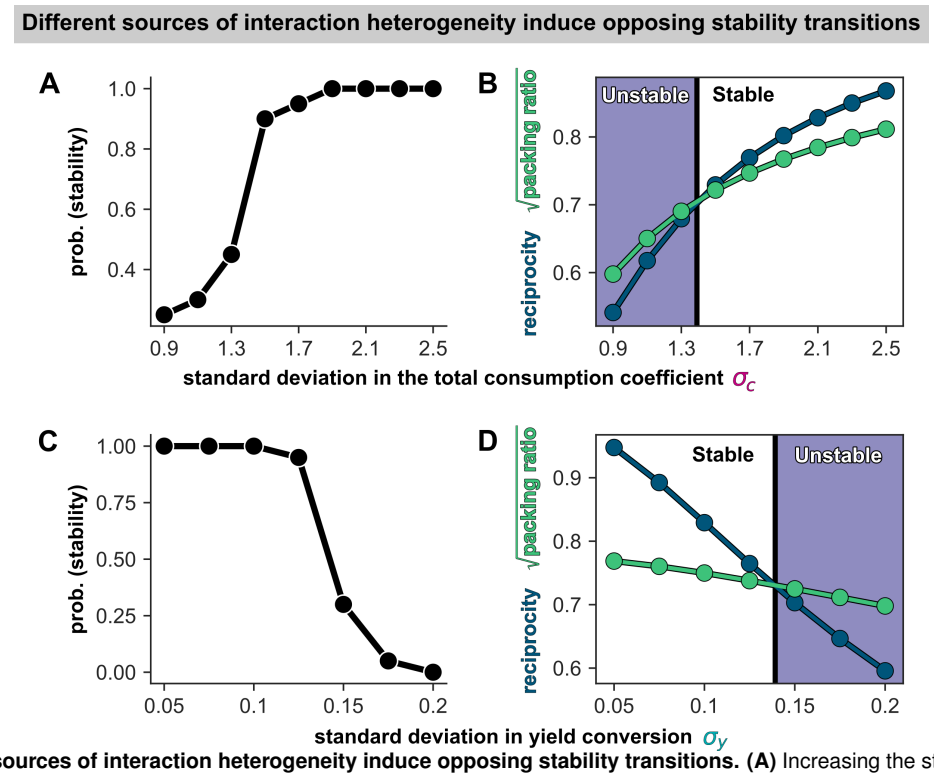

Figure 4: **Different sources of interaction heterogeneity induce opposing stability transitions. (A)** Increasing the standard deviation (and equivalently variance) in the total consumption coefficient stabilises community dynamics. For each point, 20 communities were sampled from the same parameter distributions and simulated. The probability communities exhibited stable dynamics was determined by the proportion of communities with numerically-estimated maximum Lyapunov exponent less than 0. All parameters were the same as fig. 3, except $M = 200$ and $\mu_c = 160$. **(B)** Increasing σ_c stabilises communities by increasing the growth-consumption correlation faster than the $\sqrt{\text{packing ratio}}$. The numerically-solved values of the analytically-derived correlation (dark blue), packing ratio (green) and stability boundary (black). **(C)** Increasing the standard deviation in the yield conversion factor destabilises community dynamics. Same simulation protocol as (A). **(D)** Increasing σ_y destabilises communities by decreasing the growth-consumption correlation faster than $\sqrt{\text{packing ratio}}$.

Having shown that large resource pools actually generate communities with high species diversity and stable dynamics, we sought to answer a related question: Does increasing heterogeneity in consumer-resource interactions destabilise communities, regardless of the mechanisms generating it? This prediction comes from both resource-implicit and -explicit models. Resource-implicit models predict that increasing heterogeneity in species interactions destabilises communities [25–27, 29], which can be achieved through increasing heterogeneity in underlying consumer-resource interactions. This is easily observable for the special case where resource dynamics equilibrate faster than species dynamics, which reduces the consumer-resource model to the resource-implicit gLV model

[50, 52, 62] (SI Appendix E). Similarly, previous studies in resource-explicit models showed that increasing heterogeneity in consumer-resource interactions (by increasing variance in consumption and growth coefficients) destabilises communities by increasing the packing ratio [52]. We tested this prediction in our model by varying two key parameters that have similar effects on consumer-resource interaction heterogeneity: the variance in consumption coefficient (σ_c^2) and the variance in the yield conversion factor (σ_y^2). Contrary to expectation, varying these parameters induced opposing stability transitions. While high variance in yield conversion destabilised communities (Fig. 4 C), high variance in consumption coefficient surprisingly stabilised community dynamics (Fig. 4 A). These results show that the *source* of heterogeneity in consumer-resource interactions — not the presence of variation alone — determines community stability.

To understand why variance in consumption and yield conversion had opposing effects on stability, we again turned to our stability condition. At low consumption variance, $\sqrt{\text{packing ratio}}$ was larger than reciprocity, placing communities in the unstable region (Fig. 4 A, right). Increasing σ_c^2 increased both reciprocity and $\sqrt{\text{packing ratio}}$, but reciprocity increased faster, which ultimately stabilised communities (Fig. 4 B). Change in yield variance (σ_y^2) showed the opposite effect on the stability condition. When σ_y^2 was low, reciprocity was larger than $\sqrt{\text{packing ratio}}$, making communities stable. Increasing σ_y^2 decreased both quantities, but reciprocity declined faster until it became smaller than $\sqrt{\text{packing ratio}}$, destabilising community dynamics (Fig. 4 D). Therefore, our results reveal that the different biological sources of interaction heterogeneity drive opposing stability transitions.

Discussion

Robert May's foundational work [25, 26, 28] and the competitive exclusion principle [49–51] together predict that increasing resource diversity should destabilise communities (Fig. 1 C). We tested this prediction in a consumer-resource model where species growth and resource consumption are coupled through a yield conversion factor. Contrary to the expectation, large resource pools generated stable, species-rich communities, demonstrating that resource-driven diversity can be intrinsically stabilising. We also tested whether high interaction heterogeneity always destabilises communities, as suggested by previous resource-explicit models [52, 56] and indirectly by resource-implicit models [27–29]). We instead found that different sources of heterogeneity induced opposing stability transitions: While increasing variance in yield indeed destabilised community dynamics, increasing variance in consumption stabilised communities. These findings reveal that resource dynamics and the biological mechanisms coupling them to species dynamics can invert classical relationships between species diversity or interaction heterogeneity and stability.

Our results differ from May's predictions because resource-implicit and explicit models have different stability criteria. In resource-implicit models, communities become unstable when the total strength of inter-species interactions exceeds self-inhibition. This occurs when species diversity and interaction heterogeneity are high [25–27, 29], when the average inter-species interaction strength is strong, and when interaction networks are highly connected [23–26, 29]. Resource-explicit and resource-implicit models become equivalent only under special conditions: e.g.,when resource dynamics are much faster than species dynamics and are thus "driven" by species dynamics [50, 62, 70–72]. In our work, explicit resource dynamics drives the positive resource diversity-stability relationship, even when consumer self-inhibition is additionally imposed to more closely match May's model (see SI Appendix E). When resources actively drive community dynamics, communities become unstable when the correlation between growth and consumption is lower than $\sqrt{\text{species packing ratio}}$, meaning that consumers encroach on each other's niches [52, 56, 57]. Arguably, this condition appears conceptually similar to May's — since consumer's encroaching on each other's niches effectively intensifies inter-species competition relative to self-inhibition. However despite conceptual similarities, the inclusion of explicit resource dynamics can fundamentally change what aspects of the environment and ecological interactions promote stability. Given that most ecological communities interact strongly with their resource environment, we expect that using resource-explicit models is essential for making meaningful predictions about community stability [48].

To our knowledge, the only other mechanism that generates positive diversity-stability relationships in the resource-implicit gLV model is when species exhibit sublinear growth, rather than logistic growth as is widely assumed [22]. However, as far as we are aware, sublinear growth has only been observed indirectly in ecological time series data, not directly in controlled experiments [73]. In addition, it lacks a clear mechanistic basis. For example, most resource-explicit models such as the MacArthur or Monod consumer-resource model are well-approximated by logistic [64] or superlinear, not sublinear, growth [74]. In contrast, our model is more biologically grounded. For example, consumed resources are converted into consumer biomass through yield conversion factors, a simple yet natural representation

of consumer-specific metabolism. It will be worthwhile to experimentally test our diversity-stability relationship: by increasing the resource pool size, one can test whether the frequency of observing stable, species-rich communities increases.

Our study demonstrates that resource diversity is a biologically grounded mechanism for generating stable, diverse communities. But how broadly does this mechanism apply to natural ecosystems? One limitation of our study is that we only model competitive unstructured interactions, excluding the functional groups and cross-feeding interactions common in natural and experimental communities [36, 40, 75]. However, we expect that including these features would maintain or even strengthen the diversity-stability relationship. Adding functional groups to our model would maintain the relationship within groups (as our model effectively has one functional group) but decrease niche encroachment between groups, potentially accelerating the onset of stability. Cross-feeding expands the effective resource pool as species diversity increases, which our results suggest should stabilise communities. In the future, it will be useful to understand more broadly how the plethora of resource-mediated community interactions impact the stability of complex ecosystems.

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