Resource diversity begets stability in complex ecosystems

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Abstract

A fundamental paradox in ecology is the relationship between species diversity and ecosystem stability: May's stability condition predicts that species diversity destabilises communities, yet many diverse ecosystems in nature are stable. Here, we show that this paradox can be resolved by explicitly considering resources, which May neglects. Specifically, May's framework and the competitive exclusion principle jointly predict that resource diversity, which promotes species diversity, should destabilise communities. However, from computer simulations and analytical calculations using the finite-size cavity method, we find the opposite: resource diversity consistently generates stable, species-rich communities. Importantly, this stabilising effect disappears when resource dynamics is neglected (set to steady state). We also show that, contrary to the prevailing belief that interaction heterogeneity is always destabilising, different biological sources of heterogeneity have opposing effects on stability. Our work provides a solution to May's paradox 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. 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]. Using these "resource-implicit models", Robert May and others suggested that species-rich communities with heterogeneous inter-species interactions are inherently unstable — known as "May's stability condition" (Fig. 1 B, [8, 25–29] although exceptions exist [22]). However, these predictions often conflict with empirical evidence where species diversity can stabilise community biomass [30, 31] and 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 resource-explicit models would reveal alternative stability relationships.

Here, we test a prediction about how resource diversity might affect stability: the competitive exclusion principle states that higher resource diversity can support more coexisting species [49–51] (Fig. 1 A). According to May's

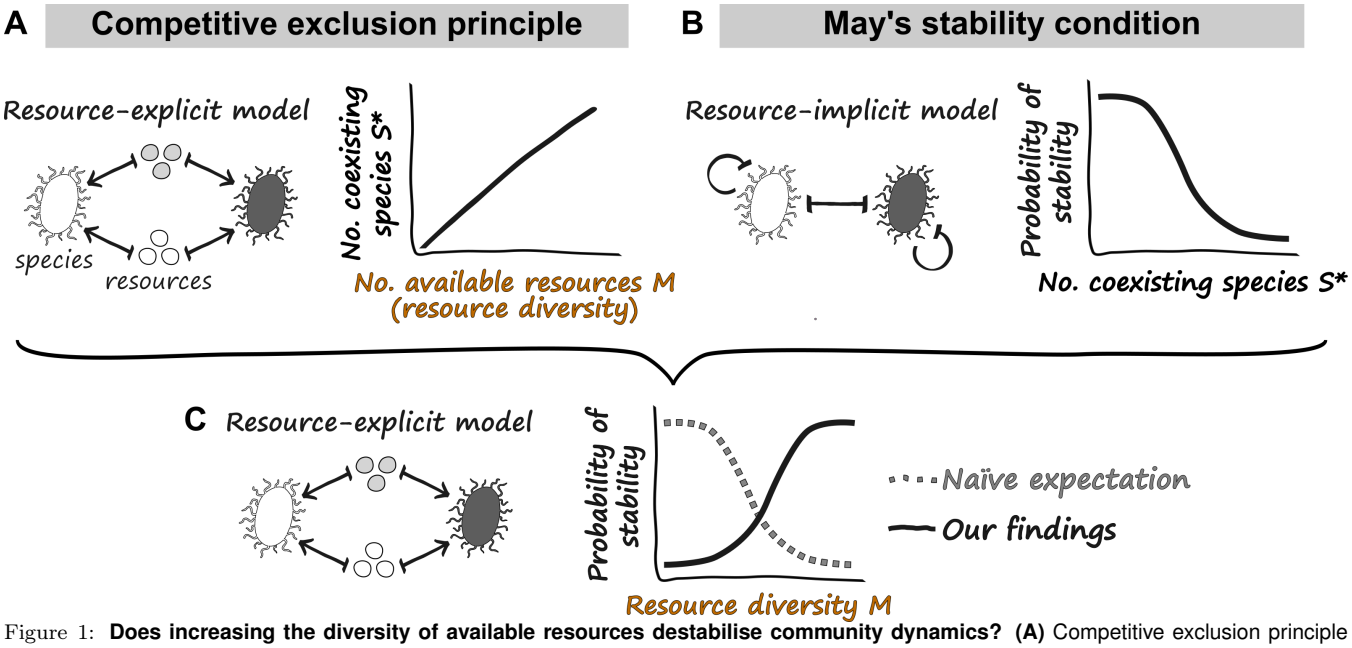

Figure 1: **Does increasing the diversity of available resources destabilise community dynamics? (A)** Competitive exclusion principle (derived from resource-explicit models): Increasing the number of available resources can support more co-existing species. **(B)** May's stability condition (derived 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).

stability condition, this higher species diversity should destabilise communities (Fig. 1 C). Specifically, 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. This positive diversity-stability relationship was driven by resource dynamics themselves, because the stabilising effect disappeared when we reduced the consumer-resource model to a resource-implicit species-only model. Given this surprising result, we 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: although high variance in yield conversion (σ_y^2) destabilised communities, high variance in consumption (σ_c^2) stabilised 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]. 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.

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:

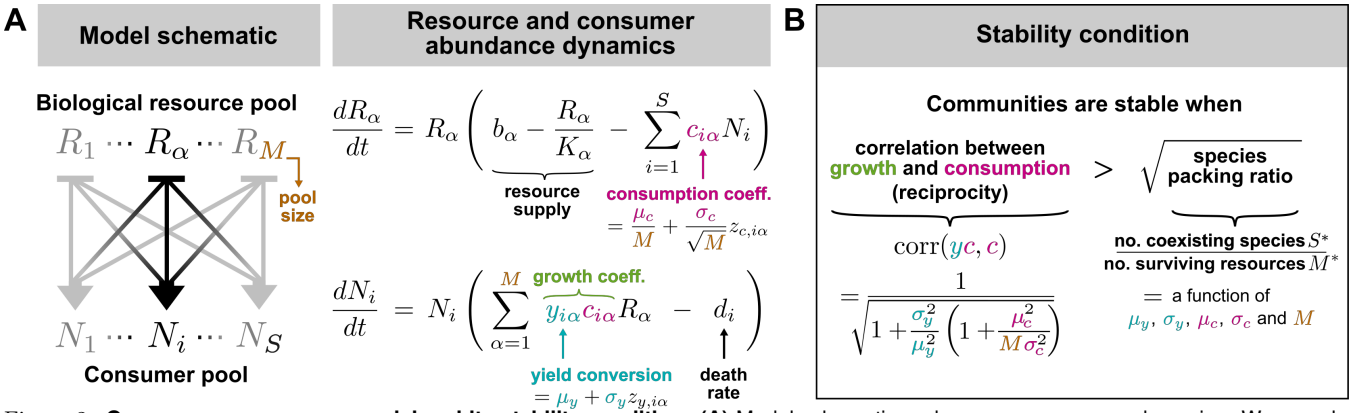

Figure 2: **Our consumer-resource model and its stability condition. (A)** Model schematic and consumer-resource dynamics. We sample yield conversion factors from a normal distribution with mean μ_y and variance σ_y^2. We sample consumption coefficients from a normal distribution with mean μ_c/M and 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^*).

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

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

Here, resources (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). Note that both resources and consumers can go extinct, and we use M^* and S^* to represent the numbers of surviving resources and consumers, respectively. 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 size affects the diversity and stability of 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 from resource-implicit models.

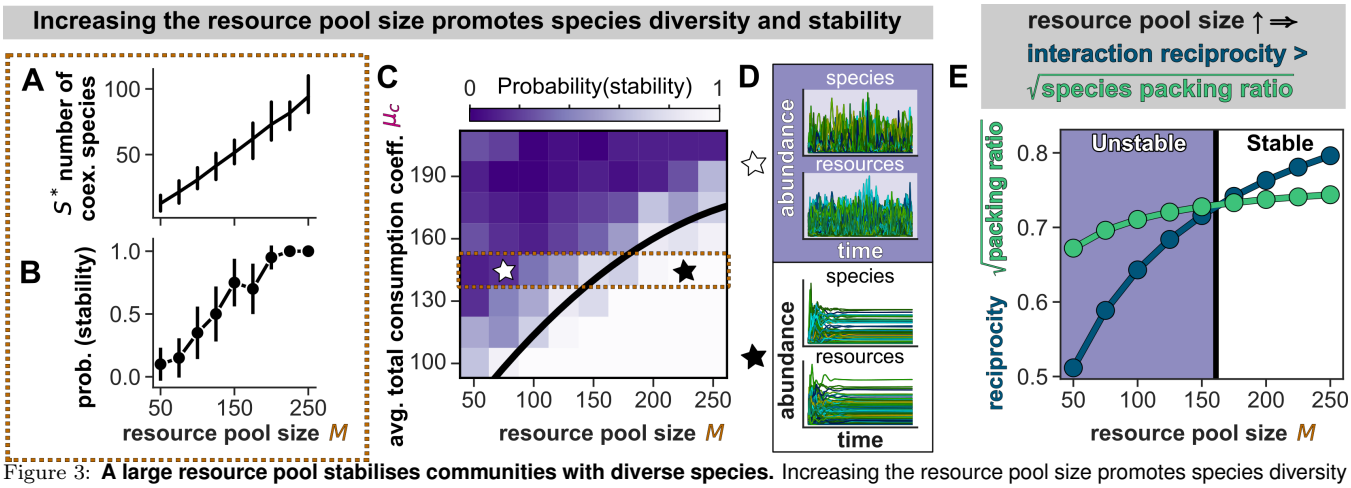

Figure 3: **A large resource pool stabilises communities with diverse species.** Increasing the resource pool size promotes species diversity **(A)** and community stability **(B)**, in direct opposition of our naïve expectation in fig. 1 C. Shown are simulations for $\mu_c = 145$, corresponding to the 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 are "well-adapted" to their metabolic niches [57]: given they have a fixed total consumption rate, high reciprocity means they predominantly consume resources that promote rapid growth. In contrast, low reciprocity means consumers are less selective about resource quality, so a greater fraction of their consumption is spent on resources that do not promote growth. The packing ratio — the ratio of surviving species to surviving resources (Fig. 2 B) — quantifies how many species coexist per resource. 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 on the same set of resources([57], SI Appendix F). For example, high reciprocity allows consumers to exploit shared resources in different ways (i.e., they occupy distinct niches), enabling them to densely pack into communities without encroaching on each other's niches; therefore, consumers stably coexist. Otherwise, consumers can continuously encroach on each other's niches, making community dynamics unstable.

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 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 reciprocity. Increasing the resource pool size raised both reciprocity and $\sqrt{\text{packing ratio}}$, but reciprocity rose much faster, eventually leading to stability (Fig. 3 E, black transition). Although the exact transition point is not fixed (e.g. can depend on a consumer's average consumption of all resources (μ_c); Fig. 3C), the qualitative picture is robust: increasing 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.

Resource dynamics are critical for large resource pools to generate stable, species-rich communities

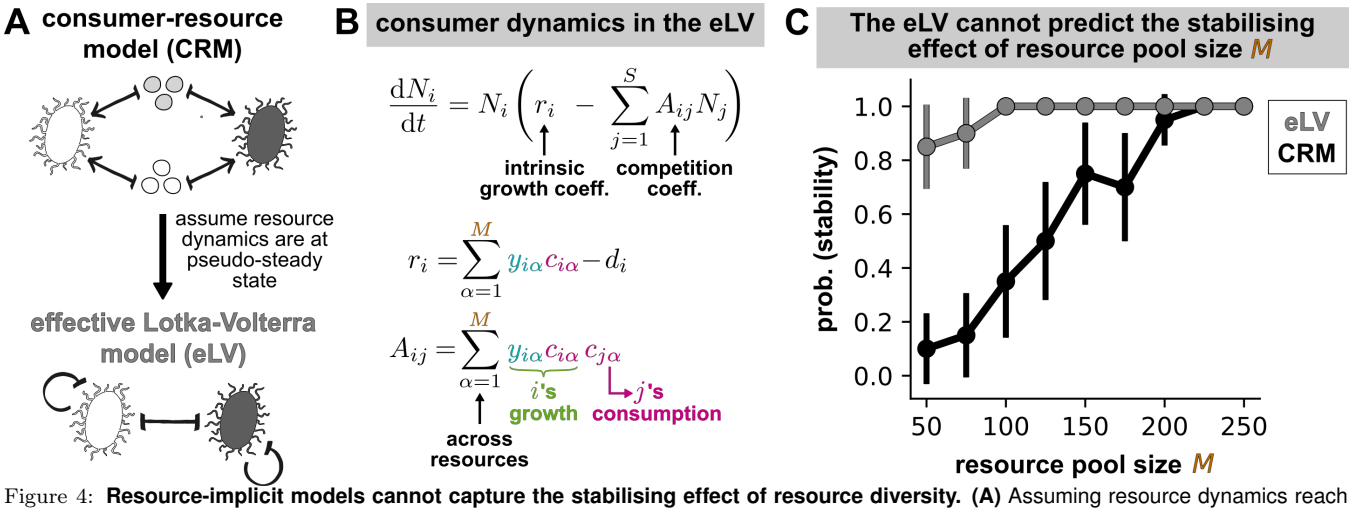

Figure 4: **Resource-implicit models cannot capture the stabilising effect of resource diversity. (A)** Assuming resource dynamics reach pseudo-steady state (e.g., under fast resource dynamics), the resource-explicit consumer-resource model (CRM) reduces to the resource-implicit effective Lotka-Volterra model (eLV). **(B)** In eLV, species competition is direct, or resource-implicit. However, the eLV is parametrised by CRM: for example, the competition coefficient of species j on i depends on i's growth and j's consumption on shared resources. We assume that all resources survive because extinctions cannot be determined without explicitly modelling resource dynamics; results are unchanged when only surviving resources are included (SI Appendix E). **(C)** Increasing resource pool size M stabilises community dynamics in CRM (black line), but has little effect in eLV (grey line). Shown are simulations for $\mu_c = 145$. Growth and competition coefficients in eLV are parametrised from existing CRMs (SI Appendix E)

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Are resource dynamics important in driving the observed positive diversity-stability relationships? To address this question, we simulated the effect of resource pool size on stability when resource dynamics are neglected - i.e. set to pseudo-steady state which occurs, for example, when resource dynamics are fast relative to consumer dynamics. Under this scenario, the consumer-resource model reduces to a model where species compete directly, which we call an "effective Lotka-Volterra model" (eLV) (Fig. 4 A). In eLV, species' growth rates and competition coefficients are determined by their consumption and their competitors' consumption of shared resources, and not by resource abundances (Fig. 4 B). Unlike in CRM where increasing resource diversity improved stability, in eLV stability is largely unaffected by resource diversity (Fig. 4 C). Indeed, eLV's stability condition is fundamentally different to that of CRM across all resource pool sizes (SI Appendix E). Thus, resource dynamics themselves, not merely resource-mediated interactions, drive the positive relationship between resource diversity and stability.

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

Having shown the positive diversity-stability relationship, we tested whether increasing heterogeneity in interaction strength destabilises communities. This prediction comes from both resource-implicit [25–27, 29] and -explicit models [52]. Interaction heterogeneity can be achieved through increasing heterogeneity in underlying consumer-resource interactions, which is easily observable for the special case where consumer-resource model is reduced to eLV [50, 52, 62] (SI Appendix E).

Contrary to expectation, increasing the variance in consumption coefficient (σ_c^2) and the variance in the yield conversion factor (σ_y^2) induced opposing stability transitions. While high variance in yield conversion destabilised

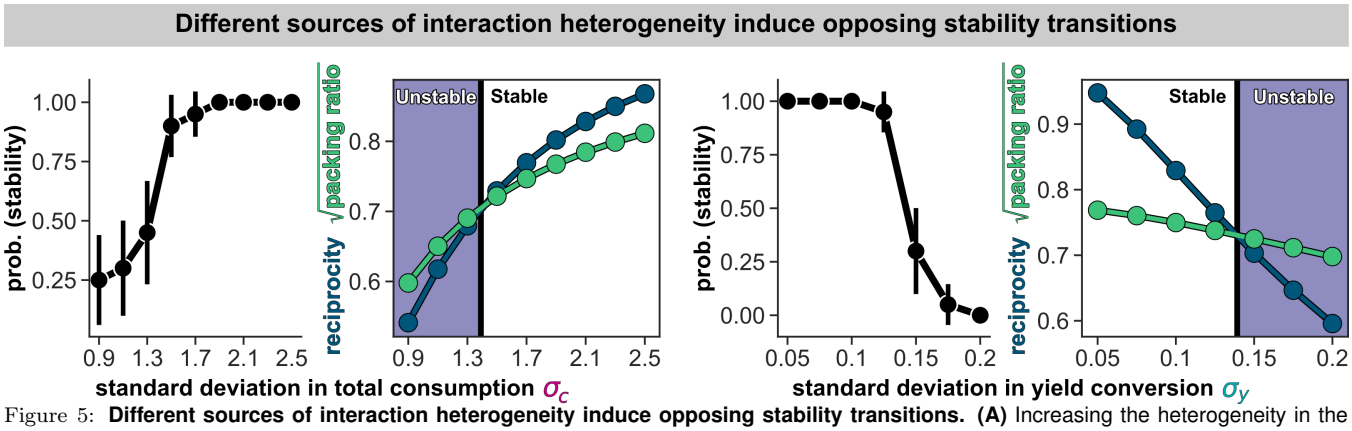

Figure 5: **Different sources of interaction heterogeneity induce opposing stability transitions.** **(A)** Increasing the heterogeneity in the total consumption coefficient stabilises community dynamics. **(B)** Increasing σ_c stabilises communities by increasing the growth-consumption correlation faster 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 heterogeneity in the yield conversion factor destabilises community dynamics. **(D)** Increasing σ_y destabilises communities by decreasing the growth-consumption correlation faster than $\sqrt{\text{packing ratio}}$. 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 $\mu_c = 160$.

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communities (Fig. 5 C), high variance in consumption coefficient surprisingly stabilised community dynamics (Fig. 5 A).

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. 5 B). Increasing σ_c^2 increased both reciprocity and $\sqrt{\text{packing ratio}}$, but reciprocity increased faster, which ultimately stabilised communities (Fig. 5 B). Increasing yield variance (σ_y^2) showed the opposite effect: When σ_y^2 was low, reciprocity exceeded $\sqrt{\text{packing ratio}}$, 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. 5 D). Together, the *source* of heterogeneity in consumer-resource interactions — not the presence of variation alone — determines community stability.

Discussion

Robert May's stability condition[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 (Fig.), and this stabilisation is driven by resource dynamics (Fig.). We also 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 (Fig.). Overall, 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]. Although resource-explicit models can be reduced to resource-implicit models when, for example, resource dynamics are much faster than species dynamics and are thus "driven" by species dynamics [50, 62, 70–72], this equivalence does not hold in our work. When we assumed fast resource-dynamics in the consumer-resource model, the effective Lokta-Volterra model could not produce the stability transitions of the resource-explicit model (Fig. 4). Therefore, the positive diversity- stability relationship, as well as other stability transitions, were actively driven by resource dynamics. In this regime, 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]. 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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