# Metabolic Trade-offs can Reverse the Resource-Diversity Relationship

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## Abstract

For species that partition resources, the classic expectation is that increasing resource diversity increases species diversity. On the other hand, for neutral species, competing equally for a single resource, diversity reflects a balance between the rate of introduction of novelty (for example by immigration or speciation) and the rate of extinction. Recent models of microbial metabolism have identified scenarios where metabolic trade-offs among species partitioning multiple resources can produce emergent neutral-like dynamics. In this hybrid scenario, one might expect that both resource diversity and immigration will act to boost species diversity. Surprisingly, though, we show that the reverse may be true: when metabolic trade-offs hold and population sizes are sufficiently large, increasing resource diversity can act to reduce species diversity. This reversal is explained by a generic transition between neutral- and niche-like dynamics, driven by the diversity of resources. The inverted resource-diversity relationship that results may be a signature of consumer-resource systems exhibiting strong metabolic trade-offs.

# Introduction

Understanding the drivers of biodiversity is one of the central goals of ecology, informing the conservation, restoration, and potentially the design and manipulation of complex ecological communities. Theory based on the differentiation of species emphasizes the role of distinct species niches, for example deriving from specialization on different resources (Chase and Leibold, 2009; MacArthur, 1972; MacArthur and Levins, 1964, 1967; Tilman, 1982). These differences can act to stabilize the coexistence of diverse communities (Levine and HilleRisLambers, 2009; Schoener, 1974; Tilman, 1982). Diversity in this view is strictly bounded by the number of limiting factors in the environment, a classic result known as the competitive exclusion principle (Levin, 1970; MacArthur and Levins, 1964). Thus, a fundamental prediction of niche-based theories is that increasing niche (e.g. resource) diversity should drive increased species diversity (Dal Bello et al., 2021; MacArthur, 1972; Tilman, 1982). But historically, it has been a challenge to reconcile the competitive exclusion principle with the remarkable diversity of natural communities. Hutchinson famously articulated this problem as the "paradox of the plankton" (Hutchinson, 1959), although the paradox applies equally to tropical rainforests (Wright, 2002), soil microbial communities (Torsvik et al., 2002), and other hyperdiverse ecosystems where many species coexist on apparently few resources or other limiting factors.

Neutral theories, on the other hand, posit that species differences are unimportant for ecological dynamics, and consequently that communities are governed by the stochastic drift of ecologically equivalent species (Chave, 2004; Hubbell, 2001, 2005). Neutral theories predict that the key determinants of diversity are the rate of introduction of novel species (via speciation or immigration) and the total community size (Chave, 2004; Haegeman and Loreau, 2011; Hubbell, 2001; Woodcock et al., 2007). These models evade Hutchinson's paradox, because diversity can be arbitrarily high given frequent enough introduction of novelty in a large enough group of individuals. Beyond their consistency with high species richness, simple neutral models have surprising power to explain biodiversity patterns in a range of ecosystems (Bell, 2000; Hubbell,

2001; Volkov et al., 2003; Woodcock et al., 2007). However, these successes are surprising precisely because the equivalence assumption at the heart of neutral theories seems plainly incompatible with well-documented trait differences between species (Purves and Turnbull, 2010), which result in well-characterized differential resource use and habitat associations (D'Andrea et al., 2020b; Schoener, 1974; Webb and Peart, 2000; Zeng et al., 2022), and apparently non-neutral dynamics (Clark and McLachlan, 2003; Fargione et al., 2003; Levine and HilleRisLambers, 2009; Wootton, 2005).

One possible resolution to these tensions is the emergence of neutral-like dynamics and biodiversity patterns in fundamentally non-neutral communities (Gravel et al., 2006; Haegeman and Loreau, 2011; Holt, 2006). Such communities might exhibit neutral-like dynamics for many species at steady-state, while revealing non-neutral responses to large perturbations and differences in ecologically-relevant traits measured "out of context". Models incorporating both species trait differences and stochastic factors have been used to show how and when drift can dominate niche-driven dynamics (D'Andrea et al., 2020a; Fisher and Mehta, 2014; Gravel et al., 2006; Haegeman and Loreau, 2011). These models demonstrate that neutral-like outcomes can persist when the strict assumption of ecological equivalence is broken, but they typically require that species differences are very small (D'Andrea et al., 2020a; Fisher and Mehta, 2014), or that sets of very similar species are selected through the model dynamics before neutrality emerges (D'Andrea et al., 2020b; Holt, 2006).

A more far-reaching possibility is that fitness trade-offs might produce neutral dynamics even in communities with substantial interspecific trait differences, by equalizing per capita demographic rates at steady state (Hubbell, 2005, 2006; Lin et al., 2009; Ostling, 2012). Posfai, Taillefumier, and Wingreen recently studied a simple consumer-resource model where the imposition of metabolic trade-offs produces exactly this behavior (Erez et al., 2020; Posfai et al., 2017). In their model, consumers face an allocation constraint limiting their ability to grow on different substitutable resources, and as a result the community can drive resource availability to a point where any number of consumers have equal fitness. Posfai et al. showed that a deterministic

version of this model violates the competitive exclusion principal, although the resulting equilibrium community is not stabilized against all small perturbations, as usually required for stable coexistence. Instead, the model possesses neutral directions along which species abundances can drift, and in a stochastic version of the model, neutral dynamics emerge. This model has inspired significant interest, particularly in microbial ecology, where there has been a productive effort to relate aspects of cellular metabolism, such as enzyme allocation constraints, to community dynamics (Ferenci, 2016; Harcombe et al., 2014; Litchman et al., 2015; Muscarella and O'Dwyer, 2020; Pacciani-Mori et al., 2021).

Models of emergent neutrality raise important new questions. Chief among these is what factors control biodiversity in such ecosystems. Does the diversity of resources affect the diversity of consumers, as predicted by niche theories, or is this relationship severed by the emergence of neutral dynamics? Do resource diversity, immigration rate, and system size act separately to shape consumer diversity, or in concert? Using the model of Posfai et al., we explore these questions in a scenario where neutrality emerges from metabolic trade-offs. We find that the interaction of niche and neutral processes can lead to new and unexpected resource-diversity relationships, including a regime where consumer diversity typically decreases with larger numbers of resources, a behavior not predicted by either theory alone. We show that this phenomenon results because communities transition between niche and neutral dynamics depending on the diversity of resources. In the process, we use theoretical results from stochastic geometry to clarify the conditions under which trade-offs may be expected to generate emergent neutrality.

# Model background

## *Metabolic trade-off model*

We briefly review the model introduced by Posfai et al. (2017), which is a standard consumer-resource model (Cui et al., 2020; Tilman, 1982) with an added metabolic trade-off. In this model, $m$ consumer species compete for $p$ resources which are abiotic, substitutable, and externally-

supplied at rates $\boldsymbol{s} = (s_1, \ldots, s_p)$. Each consumer $\sigma$ utilizes resource $i$ at a rate $\alpha_{\sigma i} \geq 0$. Assuming $\alpha_{\sigma i}$ is proportional to species $\sigma$'s investment in utilizing resource $i$ — for example, its production of enzymes for importing and metabolizing this resource — Posfai et al. modeled an allocation trade-off by imposing the constraint $\sum_{i=1}^{p} \alpha_{\sigma i} = E$, where $E$ is a fixed investment budget (e.g. protein synthesis budget) shared by all species. We refer to $\boldsymbol{\alpha}_\sigma = (\alpha_{\sigma 1}, \ldots, \alpha_{\sigma p})$ as the metabolic strategy of consumer $\sigma$, and the set of allowable metabolic strategies as the metabolic simplex. In a sufficiently large system, these dynamics are well-described by the deterministic model

$$\begin{aligned} \frac{dc_i}{dt} &= s_i - r_i(c_i(t)) \sum_\sigma \alpha_{\sigma i}\, n_\sigma(t) \\ \frac{dn_\sigma}{dt} &= n_\sigma(t) \left( \sum_i \alpha_{\sigma i}\, r_i(c_i(t)) - \delta \right) , \end{aligned} \tag{1}$$

where $c_i$ is the concentration of resource $i$ and $n_\sigma$ is the abundance of consumer $\sigma$. The rate at which resource $i$ is consumed depends on its concentration through the function $r_i$, which is often modeled as a linear (Type I) or Monod (Type II) function, although the qualitative behavior of the model is unchanged for any choice of $r_i$ that is smoothly increasing and satisfies $r_i(0) = 0$. All consumers experience mortality (or wash-out from the system) at a rate $\delta$. For clarity, we neglect resource loss (due to degradation or outflow) and potential differences in the "investment cost" or "value" of different resources. None of these more general (and more realistic) features affect the qualitative behavior of the model, so our main conclusions hold when they are accounted for (see SI Section 1 for additional details).

## *Model dynamics*

In the absence of the trade-off constraint, no more than $p$ consumer growth rates can generally become zero simultaneously, as required for coexistence of the consumers at equilibrium. This is precisely the competitive exclusion principle (Levin, 1970; MacArthur and Levins, 1964). The metabolic trade-off, however, implies that when all resources are available in equal concentrations, all consumers have equal per capita growth rates, and, in particular, there is a point where any number of consumers have zero net growth (achieved where $r_i = \delta/E$ for all $i$). Thus,

coexistence of $m > p$ consumers becomes possible.

In order for coexistence to be realized, however, the resource rates of change must also vanish. This requires the consumer abundances, $\boldsymbol{n} = (n_1, \ldots, n_m)$, to satisfy the linear system

$$A^T \boldsymbol{n} = (E/\delta)\boldsymbol{s}, \tag{2}$$

where $A = (\alpha_{\sigma i})$ is the matrix of consumption rates. When $m > p$, this is an underdetermined linear system with infinitely many solutions. However, consumer abundances must be non-negative to be biologically feasible. As noted by Posfai et al., this is the case if and only if the resource supply vector (normalized to $(E/S)\boldsymbol{s}$, where $S = \sum_p s_i$) falls within the convex hull of the $m$ consumer metabolic strategies (the points $\boldsymbol{\alpha}_\sigma$) in the metabolic simplex (see Fig. 1a). If this condition is met, the dynamics of the ecosystem will always approach a point where Eq. 2 is satisfied and $r_i = \delta/E$ for all $i$. In other words, all $m$ consumers will coexist indefinitely from any initial conditions. If this condition is not met, however, there is no way for equal resource concentrations to be sustained — eventually resources will equilibrate at unequal concentrations, and at most $p$ consumers will ultimately coexist at equilibrium. Thus, the realized diversity of the community is very sensitive to whether or not the resource suply is contained in the convex hull, particularly when $m$ and $p$ are very different.

Crucially, whenever the convex hull condition above holds, there exists not just one feasible choice of $\boldsymbol{n}$ that satisfies Eq. 2, but infinitely many, comprising a neutral manifold. The dynamics of Eq. 1 converge to a point on this manifold that depends on the initial conditions. At any such point, the system is stabilized against perturbations that take consumer abundances out of the neutral manifold; the dynamics will quickly return them to it. However, there are $m - p$ neutral directions within this manifold that are not stabilized; consumer abundances are free to drift in these directions with no restoring force.

## *Stochastic models*

Once the neutral manifold is reached, random drift due to stochastic births and deaths of consumers becomes impossible to ignore, even in large systems where the deterministic model provides a very good description of the dynamics away from it. This motivates consideration of a stochastic version of the model. However, we can first simplify the dynamics by observing that, near the neutral manifold, there is a natural separation of resource and consumer timescales, such that resource concentrations typically equilibrate much faster than consumer abundances (SI Section 2; see also (D'Andrea et al., 2020a)). Even when dynamics are away from the manifold, it may be reasonable to assume a separation of time scales between the fast metabolic processes that determine resource concentrations and the slower dynamics of consumer reproduction. This allows us to define a stochastic version the trade-off model (Eq. 1), but tracking only consumer dynamics.

Taking $dc_i/dt = 0$ at all times and letting the quasi-steady-state concentrations $c_i$ be functions of the consumer abundances, the growth-rate function (before mortality) of each species becomes

$$g_\sigma(\boldsymbol{n}) \equiv \sum_i \alpha_{\sigma i}\, r_i(c_i(\boldsymbol{n})) = \sum_i \alpha_{\sigma i} \frac{s_i}{\sum_\kappa \alpha_{\kappa i} n_\kappa(t)}\,. \tag{3}$$

From Eq. 3, the combined growth rate of all consumers is simply $\sum_\sigma g_\sigma(\boldsymbol{n}) n_\sigma = \sum_i s_i = S$, the total resource supply rate. Therefore we expect the total abundance of all consumers to quickly reach $\sum_\sigma n_\sigma = S/\delta$, where growth and mortality are balanced. Taking all of these considerations into account, we define a stochastic birth-death model where the total number of individual consumers is fixed at $S/\delta$. At each time step, a random individual dies and is replaced by the offspring of another individual, chosen through a weighted lottery where species with higher growth rates are more likely to be sampled. More precisely, the probability that the new individual is from species $\sigma$ is given by $g_\sigma(\boldsymbol{n}) n_\sigma / \sum_\kappa g_\kappa(\boldsymbol{n}) n_\kappa$. Away from the neutral manifold — or in the absence of one — the dynamics of this stochastic process closely track the (consumer) dynamics of Eq. 1, provided $S$ is sufficiently large. However, as the system approaches the neutral manifold, where $g_\sigma(\boldsymbol{n}) = \delta$ for all $\sigma$, the deterministic dynamics slow to a halt, while

the stochastic model continues to drift randomly (Fig. 2). Here, the model exhibits emergent neutrality.

This birth-death (BD) model is a discrete, stochastic version of the deterministic Posfai model (Eq. 1). The nature of the BD model entails that drift will eventually carry all but one species to extinction. On long time scales, however, diversity can be maintained by the arrival of new species, due to either speciation or immigration from outside the system (henceforth, we refer only to immigration for simplicity). Thus, to investigate steady-state biodiversity we follow Posfai et al. and also consider a version of the model with immigration — a birth-death-immigration (BDI) model, which is exactly like the BD model, except that at each time step the deceased individual may be replaced by a new species, bearing a new metabolic strategy, with probability $\nu$. Otherwise, with probability $1 - \nu$, the new individual is sampled from within the community, proportionally to growth rates. In our simulations of both models (BD and BDI), we sample all consumer metabolic strategies uniformly and independently from the metabolic simplex.

## Results

In the BDI model, consumer diversity reaches a dynamical equilibrium, or steady state, where novelty and extinctions are balanced. Thus, we can ask how resource diversity and consumer diversity are related in the BDI model, with and without metabolic trade-offs (Fig. 3). We summarize consumer diversity in two complementary ways: by plotting the rank-abundance curve for consumer communities, and by counting the number of consumer species (richness). When consumption rates are sampled independently, with no trade-off between rates, we find that steady-state biodiversity increases steadily with larger numbers of resources, as predicted by classic theory. Across 50 replicate systems, each with a fixed resource supply ($s$) chosen at random, communities with more resources exhibit flatter rank-abundance curves, indicating a more even composition (Fig. 3a), as well as higher overall species richness (Fig. 3b).

Surprisingly, when we repeat the same simulations with a metabolic trade-off, we observe the

exact opposite pattern. In this case, communities with more resources typically exhibit steeper rank-abundance curves (Fig. 3c) and fewer total species (Fig. 3d). For the parameters we considered, the median richness with $p = 2$ is nearly double the richness of the communities with $p = 16$ (27 versus 14 species, respectively).

Neither niche nor neutral theories can account for this striking inversion of the resource-diversity relationship. Instead, this outcome emerges from the interplay of niche and neutral dynamics in the metabolic trade-off model. Comparing our BDI simulation results against a purely neutral model with the same system size and immigration rate ($\nu$), we find that the diversity summaries in communities with only 2 resources are almost indistinguishable from the neutral model, while communities with 16 resources appear markedly non-neutral (Fig. 3c-d). This suggests that the dynamics may be more niche- or neutral-like as a function of resource diversity.

To investigate this idea, we next examined the persistence of diversity in the model without immigration (BD model). In the BDI model, steady state diversity reflects a balance between species lost to extinction and gained through immigration. Because the immigration process has no dependence on the number of resources, we hypothesized that the negative relationship between resource diversity and consumer diversity must arise due to differences in the persistence of species. To isolate the effect of resource diversity on the persistence of consumer diversity, we simulated the BD model with different numbers of resources and a constant number of consumers and recorded the time to the first consumer extinction across many replicate communities. The time to first extinction provides a direct measure of how quickly diversity erodes through the dynamics. In these simulations, we vary resource diversity, but initial consumer diversity, initial consumer population sizes, and overall resource supply are held constant. We considered two different resource supply scenarios: one where the inflow rates of different resources are chosen uniformly at random from a simplex, with the total resource supply $S$ fixed (mirroring our BDI simulations), and a simplified scenario where all resources are supplied at equal rates.

Fig. 4 shows the distribution of times to first extinction for each value of $p$ in each of these

two scenarios. The results are presented in survival plots, showing the fraction of communities where no extinction has happened up to a given time (the complement of the cumulative distribution function). While there are quantitative differences between the two resource supply scenarios, the qualitative pattern is the same: the time until an extinction is typically longer in communities with fewer resources. This effect is especially pronounced in the random resource supply scenario where, after 50 time units, almost every community with 8 or 9 resources has experienced an extinction, while nearly half of communities with 2 resources remain intact.

We expect that the time to first extinction depends strongly on whether dynamics are niche-like or neutral. In the absence of emergent neutrality, a subset of species with lower fitness — corresponding to those excluded in the deterministic version of the model dynamics (Eq. 1) — experience a biased random walk toward zero abundance (as in Fig. 1b). These species will typically be excluded much faster than those experiencing a neutral (unbiased) random walk (Posfai et al., 2017). In the BD model, each community can be classified by whether or not the resource supply vector $\boldsymbol{s}$ is contained in the convex hull of consumer metabolic strategies, in which case we expect emergent neutrality. In Fig. 5 we plot the conditional times to first extinction, classified in this way. It is apparent that extinctions occur much more rapidly when the convex hull condition is not met. In other words, some species are lost from the community much more rapidly when there is no emergent neutrality. When the convex hull condition is met, on the other hand, the times to first extinction become much closer to a neutral reference model.

Somewhat counter-intuitively, the negative relationship between resource diversity and consumer persistence disappears once we condition on the convex hull condition. The results within each case — resource supply in or out of the convex hull — conform to neutral and niche theory predictions, respectively. When the resource supply is outside the convex hull of consumer metabolic strategies, we expect niche-like dynamics, where a greater number of resources contributes to consumer coexistence. Indeed, in these cases (teal points in Fig. 5), we find that the time to first extinction is longer with more resources. When the resource supply is within the convex hull of consumer metabolic strategies the result is emergent neutrality, where resource di-

versity should have no effect on consumer persistence. As expected, in these cases (yellow points in Fig. 5, we observe little difference in extinction times between communities with different numbers of resources, and no clear trend.

How, then, does the overall negative relationship arise? Because the times to first extinction are much longer under emergent neutrality, regardless of the number of resources, the overall relationship can be explained if communities with fewer resources are more likely to satisfy the convex hull condition. This is exactly what we find. Fig. 5 shows that, as the number of resources increases, fewer simulated communities have their resource supply within the convex hull. As a result, the marginal or overall times to extinction, shown in purple, closely track the in-hull results for low resource diversity, but switch to following the out-of-hull results for larger values of $p$. This switch generates an emergent negative relationship between resource diversity and consumer community persistence.

We observe that the probability of emergent neutrality decreases with resource diversity very generally. Fig. 6 shows that with 10 consumer species in the equal resource supply scenario, nearly all communities with 2 resources exhibit emergent neutrality, compared to less than 10% of communities with 8 resources. Emergent neutrality is less likely overall in the random resource scenario, but likewise, we find it more than 75% of the time for $p = 2$, and almost never when $p = 8$. The drop-off is similarly steep for other numbers of consumer species. Thus, communities with few or many resources typically operate in very different regimes: with few resources, the convex hull condition is often satisfied, resulting in emergent neutrality and greater maintenance of diversity, while with many resources, the convex hull condition is very unlikely to hold, resulting in niche-like dynamics and fast exclusion of less fit species, despite the presence of the metabolic trade-off.

We can take advantage of the geometric formulation of the convex hull condition to better understand how the likelihood of emergent neutrality depends on $m$ and $p$. Determining the probability that a given point is contained in the convex hull of some $m$ random points in $d$-dimensional space is a well-studied problem in the field of stochastic geometry (in our context,

$d = p - 1$, the dimension of the metabolic simplex) (Bárány, 2008; Schneider, 2017). A classic result is Wendell's Theorem (Wendel, 1962), which states that if $m$ points are sampled independently from a distribution that is symmetric around a point $\boldsymbol{s}$ in $p - 1$ dimensions, then their convex hull contains $\boldsymbol{s}$ with probability

$$1 - \frac{\sum_{i=0}^{p-2} \binom{m-1}{i}}{2^{m-1}} . \tag{4}$$

This setting very nearly describes our equal resource supply scenario, where $\boldsymbol{s}$ lies at the center of the metabolic simplex (Wang et al., 2023). Strictly speaking, the uniform distribution on the metabolic simplex does not satisfy the symmetry assumption in Wendell's Theorem, but we find that Eq. 4 accurately predicts the probability of finding emergent neutrality in the equal resource supply scenario across range of $m$ and $p$ values (Fig. 6).

Calculating the same probability for the random resource supply scenario, where $\boldsymbol{s}$ is also sampled uniformly from the metabolic simplex, turns out to be a substantially harder problem, and only asymptotic approximations or complex integral formulas are known (Affentranger and Wieacker, 1991; Bárány, 2008; Dwyer, 1988; Efron, 1965). However, we can still can derive some insight from Wendell's Theorem, which is known to provide an upper bound for the probability in this case (in fact, Eq. 4 provides an upper bound for *any* choice of $\boldsymbol{s}$ and *any* distribution of the consumer metabolic strategies) (Wagner and Welzl, 2001). Additionally, when $p$ is substantially smaller than $m$, a better upper bound is given by

$$\left(\frac{m-1}{m+1}\right)^{p-1} , \tag{5}$$

which we derive in SI Section 3 and plot in Fig. 6.

These formulas confirm that, regardless of the resource supply scenario, the convex hull condition (and thus emergent neutrality) is likely to hold when there are few resources compared to the number of consumers ($p \ll m$), and very unlikely when the number of resources approaches the number of consumers ($p \approx m$). Furthermore, as $m$ and $p$ become large, Eq. 4 exhibits a threshold behavior: the probability of finding emergent neutrality in the equal resource scenario drops sharply from close to one for $p < m/2$, to close to zero for $p > m/2$. In the random

resource supply scenario, this probability falls off much faster; Eq. 5 shows that it shrinks at least exponentially as $p$ increases (Fig. 6). In fact, for ecosystems with many species, the random supply scenario also exhibits a probability threshold, but the threshold value is much smaller than $m/2$ (proportional to $\log(m)$) (Dyer et al., 1992; Frieze et al., 2020). Thus, we should only expect to observe emergent neutrality in this case when there are very few resources, and in general, regardless of how $\boldsymbol{s}$ and $\boldsymbol{\alpha}_\sigma$ are distributed, Wendell's Theorem tells us that emergent neutrality is very unlikely when $p > m/2$.

## Discussion

Fitness trade-offs, such as the metabolic trade-offs considered here, may provide a general mechanism by which neutral dynamics can emerge in communities with functionally dissimilar species. Posfai et al. demonstrated this possibility using a simple consumer-resource model, motivated by the ubiquitous allocation constraints that govern metabolic strategies in bacteria, phytoplankton, and many other organisms (Ferenci, 2016; Litchman et al., 2015). However, this model can exhibit both niche- and neutral-like dynamics, depending on the specific resource supply and consumer metabolic traits. By investigating a stochastic version of the trade-off model — with and without immigration — we found that niche and neutral dynamics typically arise in different parameter regimes. Surprisingly, the interplay of these two regimes can cause a reversal of the classic positive relationship between resource diversity and consumer diversity.

To understand this counter-intuitive outcome, we showed that resource diversity plays a key role in determining the probability of observing niche- or neutral-like dynamics in the model. The fact that this transition is controlled by the number of resources — as opposed to parameters that essentially define niche and neutral regimes, such as the degree of niche overlap or stochasticity — stands in contrast to previous models of emergent neutrality (D'Andrea et al., 2020a; Fisher and Mehta, 2014). In particular, using theoretical results from stochastic geometry, we showed that emergent neutrality is very likely when resource diversity is low, with a sharp

transition from typically neutral to typically niche-like dynamics as the number of resources grows relative to the number of consumers. When dynamics are neutral, high diversity can be maintained longer, because no species decline exponentially to extinction. As a result, even though neither dynamical regime exhibits a negative resource-diversity relationship individually, the transition between high-diversity neutral dynamics with few resources and lower-diversity niche dynamics with more resources leads to an emergent negative relationship (Fig. 5), a striking example of Simpson's paradox (Simpson, 1951).

It is important to emphasize that the while the transition from neutral to niche regimes as a function of resource diversity is a very general feature of this model, the resulting resource-diversity relationship is not necessarily negative. This relationship depends on the typical properties of the two regimes themselves. In a neutral BDI model, diversity depends on the system size and immigration/speciation rate, with the expected steady-state diversity approximately equal to $-S\nu \log(\nu)$ (Chave, 2004; Hubbell, 2001). When $S$ and/or $\nu$ are large enough, diversity in the neutral regime can be much higher than in the niche regime, where it is limited by the number of resources, $p$ (in fact, the number of stably coexisting species in the niche regime is typically less than $p/2$ (Cui et al., 2020)). However, exclusion is not instantaneous in the niche regime, so steady state diversity may be higher in the BDI model, especially if $\nu$ is large. This "excess" diversity of rare species would be analogous to mutation-selection balance in population genetics. Overall, we expect that diversity will be substantially higher in the neutral regime when $-S\nu \log(\nu) > p$ and $\nu$ is small (implying $S$ is large). Conversely, diversity may actually be lower in the neutral regime if $-S\nu \log(\nu) < p$.

The framework we develop here can help predict which drivers of biodiversity might be more relevant in specific communities with metabolic trade-offs, given some knowledge of the system size, immigration rate, and resource diversity. Even in cases where the resource-diversity relationship is not completely inverted, the interplay of niche and neutral dynamics might obscure or weaken this relationship. Additionally, metabolic trade-offs might cause consumer diversity to be more sensitive to overall resource supply ($S$, which increases diversity in the neutral regime)

than to the number of resources, a pattern than has been observed empirically (Stevens and Carson, 2002).

Our theoretical analysis assumes that consumer metabolic strategies are randomly distributed and resource supply rates are fixed. The first assumption may be unrealistic if consumer strategies have evolved or can be dynamically adjusted to track resource supply (Pacciani-Mori et al., 2020). The second assumption may be violated if resource availability varies in time, for example when some resources are supplied in pulses (Erez et al., 2020; Wang et al., 2023). While a detailed analysis of these scenarios would be more involved, we expect that our broad conclusions are robust to both. Because the convex hull of a set of metabolic strategies "covers" less volume in a higher dimensional metabolic simplex, it should generally be more difficult for consumers to track the supply of many resources at once, and more likely that small changes move the resource supply out of the convex hull. Additionally, Posfai et al. showed that their convex hull condition applies to the time-average of a fluctuating resource supply, implying that our results also characterize this more general scenario, and that larger convex hulls, which are more likely with fewer resources, increase the probability of finding emergent neutrality in the presence of a fluctuating resource supply, even when consumer metabolic strategies are non-random.

It remains an open question whether the trade-off model introduced by Posfai et al. provides an adequate description of real-world consumer-resource systems. Caetano et al. (Caetano et al., 2021) have recently argued that the emergence of neutrality in this model is an artifact of the simple, linear functional form of the trade-off and consumer growth functions. However, in the SI Section 4, we show that emergent neutrality can result from trade-offs in a broad class of consumer-resource models where resources are combined linearly toward growth. Although this condition may sound restrictive, we show that this class of models includes other realistic consumer-resource scenarios, such as multiplicative co-limitation (Harpole et al., 2011; Muscarella and O'Dwyer, 2020; Saito et al., 2008), which are not obviously linear. Another question is whether real-world trade-offs are sufficiently strict to be adequately modeled by an equality constraint (Erez et al., 2020). The qualitative behavior of the Posfai et al. trade-off model — including

all of our results — is robust to small violations of the equality assumption, although sufficiently large variation in species' investment budgets will result in a loss of the neutral regime (see SI Section 5 for details). Empirical characterization of metabolic trade-offs is an active area of research, and closer integration of consumer-resource theory and biophysical constraint quantification could shed light on when and where trade-offs are strict enough to produce emergent neutrality.

We have shown that a transition between neutral and niche dynamics, and an attendant transition between qualitatively different controls on diversity, is a robust consequence of a strict metabolic trade-off. Fundamentally, the existence of such a trade-off breaks the typical relationship between resource diversity and consumer diversity because it guarantees a set of resource concentrations at which all consumers have zero net growth. Under these conditions, regardless of the specific model scenario, it is more likely that all resource derivatives vanish simultaneously if there are fewer resources. More generally, we hypothesize that any trade-off that ensures equal fitnesses under specific environmental conditions is likely to exhibit such behavior. We suggest that this transition, as well as a reversal of the relationship between niche and species diversity, are generic signatures of ecosystems where neutrality emerges from trade-offs, and could help to identify such dynamics in natural communities.

## Data and Code Availability

All code and simulation data used in this work are available at:

`https://github.com/zacharyrmiller/tradeoffs_reverse_resource_diversity`

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## Figures and captions

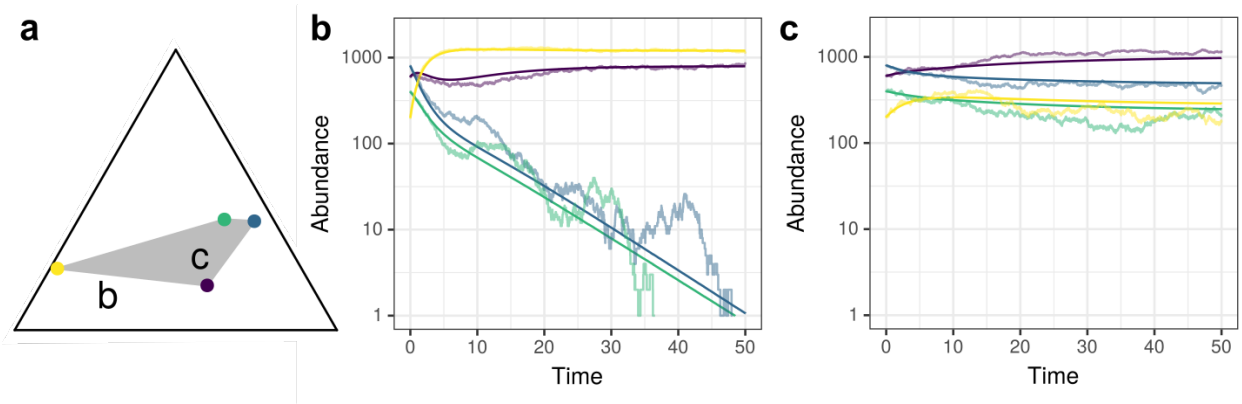


Figure 1: Convex hull condition for the consumer-resource model with trade-offs. Community dynamics depend on whether the resource supply vector falls outside or inside the convex hull of consumer metabolic strategies. (a) Metabolic strategies of four consumer species (colored points) competing for three resources are shown in the two-dimensional metabolic simplex. The convex hull of the consumer strategies is shaded gray. In (b) and (c), we show consumer dynamics corresponding to two different resource supply vectors (indicated by letters in (a)). Deterministic dynamics (solutions of Eq. 1) are indicated by dark lines, and one representative realization of the stochastic BD model is shown with light lines for each scenario. When the resource supply vector is outside of the convex hull (b), two consumer species quickly decline to extinction (at most three — the number of resources — can coexist). When the resource supply is within the convex hull (c), the dynamics approach a neutral manifold where all consumers persist.

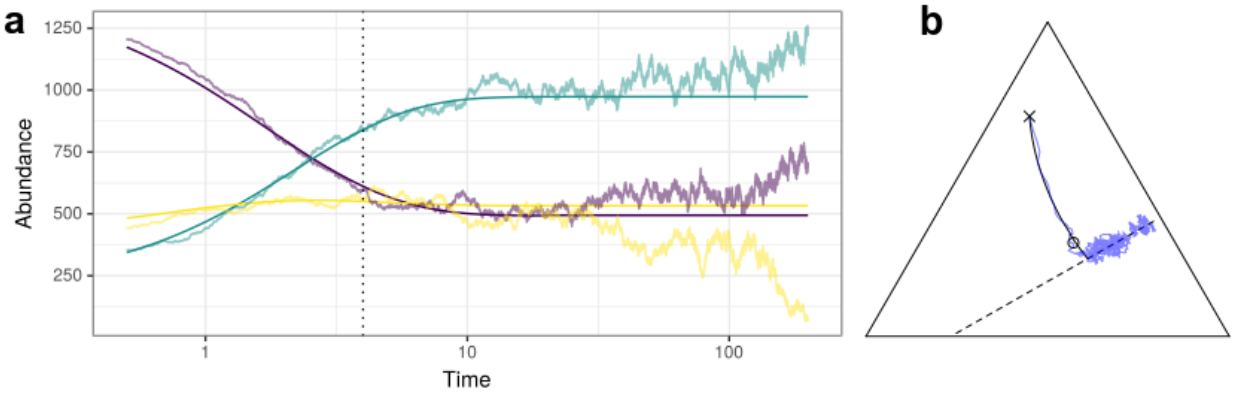


Figure 2: Emergent neutrality in the stochastic (BD) model. When the convex hull condition holds, stochastic dynamics exhibit a transient niche-like phase, followed by neutral drift. (a) An example time series for three consumers competing for two resources illustrates these distinct phases. In the first phase of the dynamics, stochastic trajectories (light lines) closely track the corresponding deterministic dynamics (dark lines) as they approach the neutral manifold; however, once the manifold is reached, the stochastic dynamics drift within its confines, while the deterministic dynamics halt. (b) The same community trajectory visualized in the space of consumer frequencies moves rapidly from the starting point (x) to the neutral manifold (dashed line), at which point the community drifts neutrally along the manifold. The approximate onset of emergent neutrality at time $t = 5$ is indicated in both panels, by a dotted line and open circle, respectively.

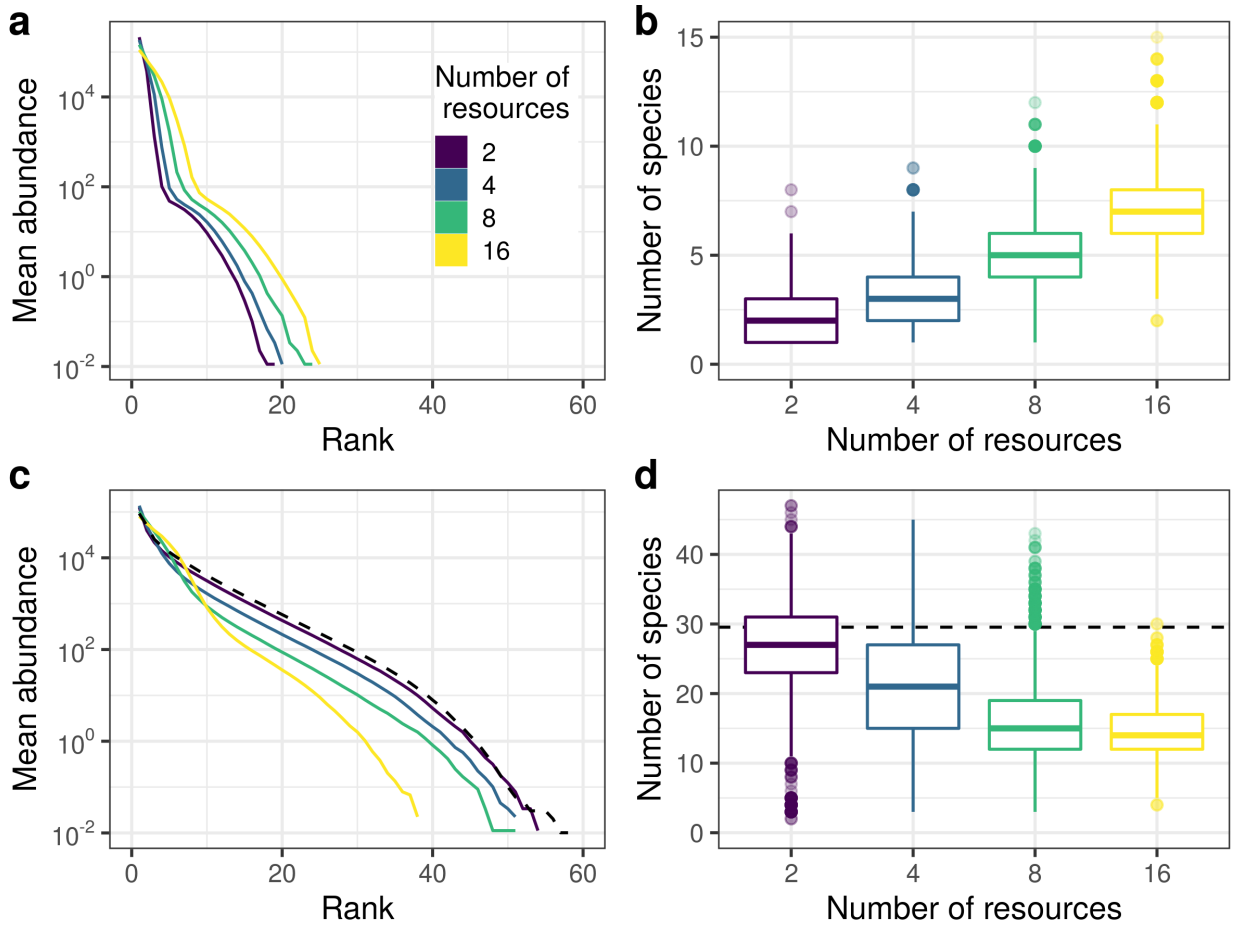


Figure 3: Relationship between resource and species diversity reverses when there are metabolic trade-offs. We plot steady state diversity statistics from the stochastic birth-death-immigration model, simulated over $10^7$ time steps. (a and c) Rank abundance curves for four different levels of resource diversity (averaged over 50 simulations), without (a) and with (c) metabolic trade-offs. (b and d) Distribution of species richness for each level of resource diversity, without (b) and with (d) metabolic trade-offs. Results from a neutral BDI model with the same total community size ($S = 5000$) and immigration/speciation rate ($\nu = 0.001$) rate are shown for comparison with the trade-off communities (black dashed lines). When a trade-off constraint is enforced, communities with more resources are typically less even and less rich.

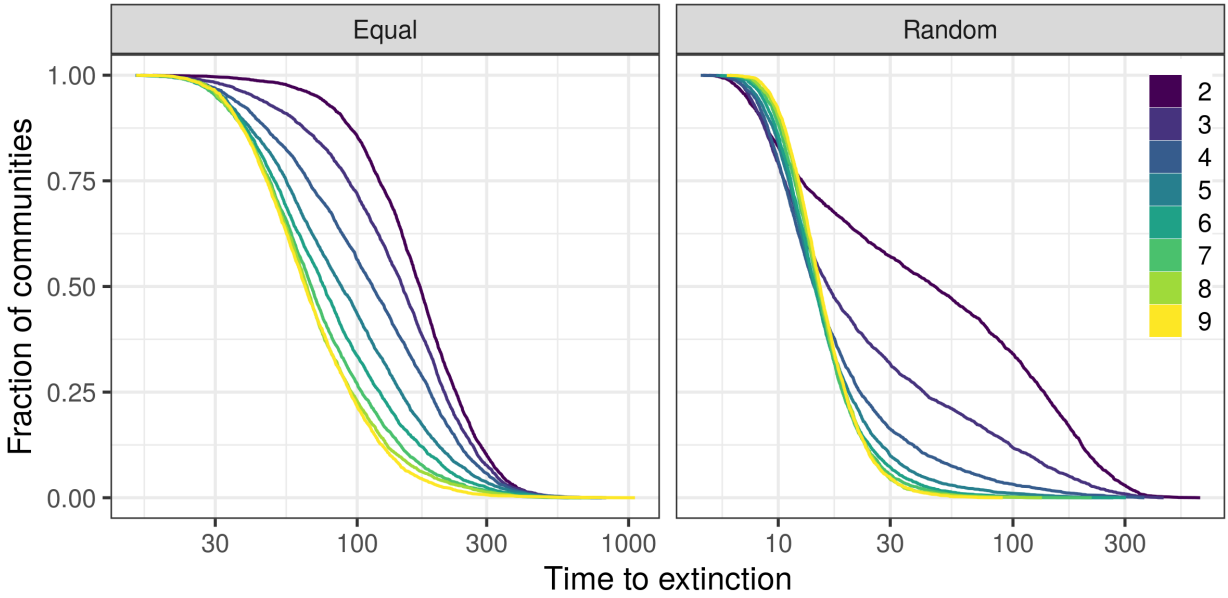


Figure 4: Survival curves show the distribution of times to first extinction in the BD model, for communities with $m = 10$ species and varying numbers of resources (colors). We consider two scenarios for the resource supply: equal supply of all resources (left), or supply chosen uniformly at random from the metabolic simplex (right). Each curve shows the fraction of communities with no extinctions up to the indicated time, summarizing 3000 stochastic realizations for each scenario and number of resources. Times are shown on a log scale. All consumers had equal initial abundances. In both scenarios, communities with fewer resources tend to persist longer before the first extinction.

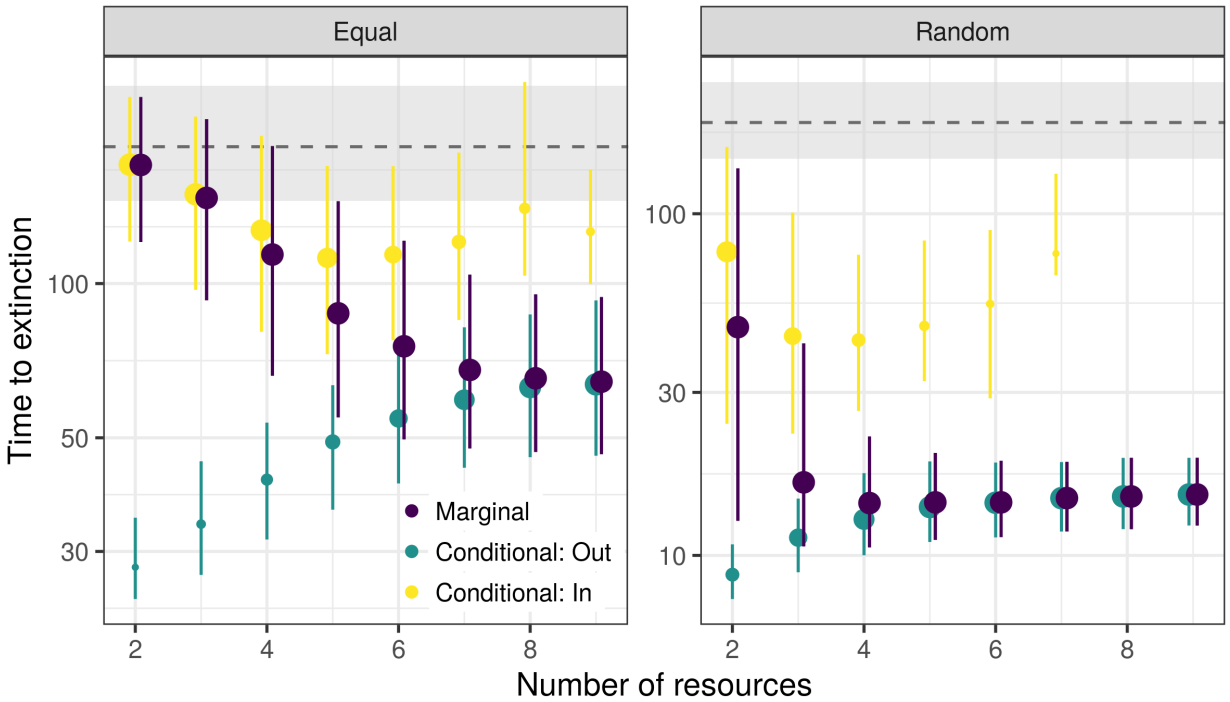


Figure 5: Times to first extinction in the BD model, classified by whether the resource supply is within (yellow) or outside (teal) the convex hull of consumer metabolic strategies. Points indicate the median value for each number of resources; error bars show upper and lower quartiles (note log scale). Point sizes are proportional to the number of observations in each category. For reference, the median (dashed line) and interquartile range (gray) are also shown for a neutral model. When the convex hull condition is met, the distribution of extinction times approaches the neutral expectation; otherwise, extinction times increase as a function of resource diversity. The marginal distribution (purple) shows an emergent negative relationship with the number of resources, resulting from a shift in which outcome is more likely as the number of resources grows.

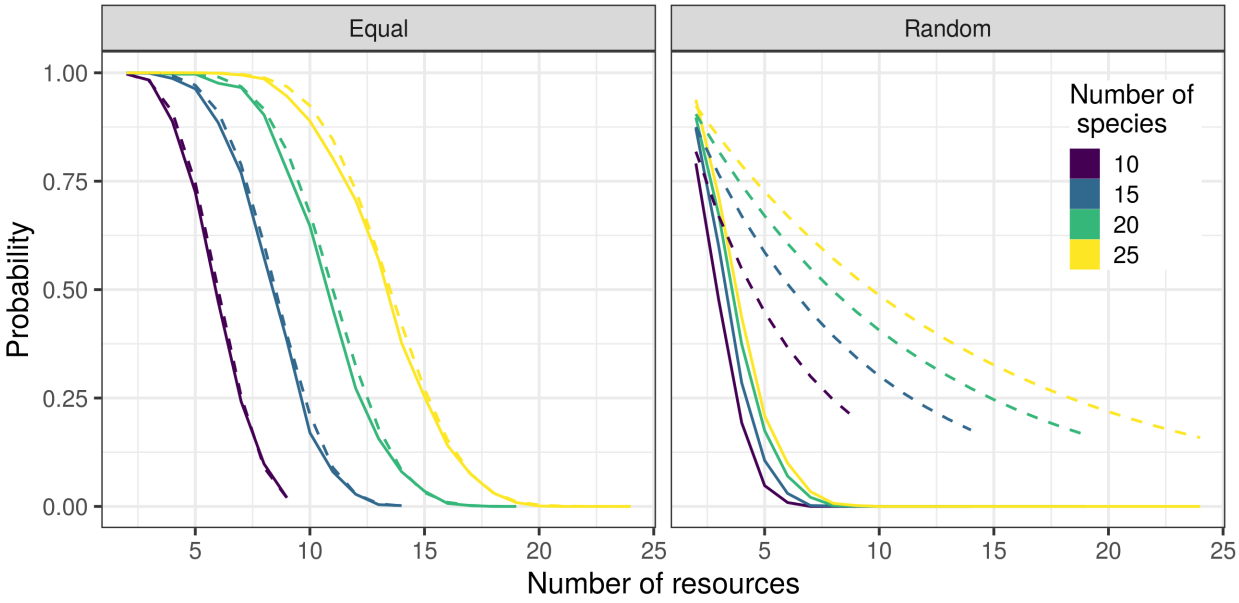


Figure 6: Probability that the resource supply vector falls within the convex hull of consumer metabolic strategies, as a function of the number of resources and consumers. When resources are supplied equally, these probabilities (solid lines) are very well approximated by Wendell's theorem (Eq. 4; dashed lines). When the resource supply vector is chosen at random, the probability of emergent neutrality is sharply reduced for the same $m$ and $p$. These probabilities fall below an exponential upper bound (Eq. 5; dashed lines), which captures the fast initial decline as resource diversity increases. The case $m = 10$ (purple) corresponds to simulations shown in Figs. 4 and 5.