Density dependence promotes species coexistence and provides a unifying explanation for distinct productivity-diversity relationships

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Abstract:

Understanding complex communities, such as microbial consortia, requires a mechanistic framework appropriate for large numbers of species. Negative density dependence is often included in population models, typically as a density-dependent mortality term, but its full impact on community structure remains unclear. Here we use mechanistic population models of resource consumption to examine the effects of negative density dependence and develop a tractable framework for understanding diversity patterns in complex systems. Using graphical analysis, we show that density-dependent mortality expands coexistence zones along resource gradients. We then derive a simple formula predicting species abundances in subsets (guilds) of a complex ecosystem, in which many species compete for a resource or share a predator, modulated by density-dependent mortality and other factors. Finally, we use our formula to explain how qualitatively distinct relationships between productivity and diversity can emerge from a generalized ecosystem description, providing new insights into previously unreconciled observed patterns.

1. Introduction

Since Hutchinson articulated the "paradox of the plankton" (Hutchinson 1961), numerous hypotheses have been proposed to explain the coexistence of a large number of plankton species competing for a limited set of resources. Resource competition theory (RCT), a foundational framework in theoretical ecology, has substantially deepened our understanding of plankton diversity (Tilman 1982; Litchman & Klausmeier 2001; Klausmeier *et al.* 2004; Litchman & Klausmeier 2008). However, analysis using RCT is typically restricted to simplified food web structures (Holt 1977; Holt *et al.* 1994; Chase & Leibold 2003), where its graphical techniques are not easily extended to consider more than a few (< 3) resources and species. Microbial communities, which contain thousands of species (or species-like equivalents) consuming a vast array of substrates (Moran *et al.* 2022), present a significant challenge to the application of this theoretical framework. To gain traction in understanding species coexistence and diversity patterns of such complex communities, we need a general, comprehensive, and mechanistic framework applicable to diverse systems with large numbers of resources and species.

Any comprehensive framework for understanding species coexistence must consider the impact of negative density dependence, the suppression of a species' net growth rate as its density increases due to multiple potential biological processes, many of which impact mortality rates, such as viral lysis (Winter *et al.* 2010; Thingstad 2022), host-specific parasitism (McPeek 1998), and soil pathogen interactions (Bagchi *et al.* 2014; Comita *et al.* 2014; LaManna *et al.* 2017a; Adler *et al.* 2018; Tuck *et al.* 2018). Density-dependent mortality in mathematical descriptions of population growth captures the dynamics of a wide range of

processes that are too uncertain or complex to explicitly describe, and thus is often utilized in studies of complex ecosystems (Bagchi *et al.* 2014; Fricke & Wright 2017; Adler *et al.* 2018; Bendik & Dries 2018; Xu *et al.* 2022). Additionally, density-dependent mortality is a well-established mechanism for resolving the paradox of the plankton because it facilitates the persistence of inferior competitors (Chesson 2000; Thingstad 2000).

Although density-dependent mortality is widely invoked to explain biodiversity maintenance across diverse ecological systems (Holt & Lawton 1993; Winter *et al.* 2010; Bagchi *et al.* 2014; Comita *et al.* 2014; LaManna *et al.* 2017b), theoretical studies grounded in mechanistic resource competition models have been more limited in their analysis of density-dependent mortality relative to empirical studies. Key questions remain unresolved: how does density dependence shape species coexistence and relative abundance patterns along gradients in resource supply? Although previous theoretical work has shown that density dependence can stabilize coexistence and allow more species to persist than there are limiting resources (Leibold 1998; Adler *et al.* 2007; McPeek 2012, 2019), most analyses have relied on low-dimensional graphical isocline approaches, and so the role of density-dependent mortality on community structure in more diverse systems remains poorly understood.

A broader and long-standing question is how biodiversity responds to changes in productivity and whether this relationship varies across geographic scales. Different productivity–diversity relationships (PDRs) have been observed, with monotonic increases and unimodal (hump-shaped) curves commonly observed (Mittelbach *et al.* 2001), prompting a range of explanatory mechanisms (Abrams 1988, 1995; Pastor *et al.* 1996; Mittelbach *et al.* 2001; Steiner & Leibold 2004; Brun *et al.* 2019). However, Adler et al. (2011) sampled 48

herbaceous plant communities across five continents and found no consistent relationship between productivity and species richness. While some individual sites showed linear or hump-shaped trends, the overall pattern lacked coherence. In contrast, Fraser et al. (2015) analyzed resource gradients more broadly, across 30 grassland sites on six continents, and found strong support for a unimodal PDR, with richness peaking at intermediate productivity at regional and global scales. Such divergent findings remain unreconciled, and also underscore the difficulty of drawing general conclusions from noisy empirical data, where contrasting patterns may additionally arise from sampling limitations. This suggests the need for a theoretical framework that can mechanistically link PDRs to trophic interactions and ecosystem structure. Ideally, such a framework would also explain how different PDRs may emerge from a general description of ecosystem dynamics.

Here, we comprehensively analyze how density-dependent mortality shapes species coexistence and relative abundance, which allows us to develop a mechanistic framework for understanding diversity in complex systems with many species. We begin by extending classic resource competition theory to reveal how density dependence modifies coexistence criteria, including its effects on resource consumption vectors and supply points. We then derive a general formula for species abundances—and thus species richness—within subsets of a complex community: a bottom-up (one shared resource) and a top-down (one shared predator) guild, applicable to systems with any number of species, such as diverse microbial consortia. Finally, we show that our general formula, combined with tradeoffs among traits, can be used to capture multiple PDRs within a unified framework, providing new insight into observed patterns.

2. Graphical analysis of simple systems

We begin by exploring how density-dependent mortality affects species coexistence in simple systems using graphical analysis, building on previous work (Leibold 1996; Chase & Leibold 2003). Specifically, we show how density-dependent mortality expands the coexistence domain in three well-known food web modules: (1) two species competing for two substitutable resources, (2) three generalists competing for two resources, and (3) a diamond food web with two prey species and one shared predator.

2.1 Two species and two resources

We first consider a food web of two species competing for two nutritionally substitutable resources. Assuming linear functional responses, species i with density N_i grows at rate μ_{ij} on resources R_j, supplied with concentration s_j and dilution rate a:

$$\frac{1}{N_1}\frac{dN_1}{dt} = \mu_{11}R_1 + \mu_{12}R_2 - m - m_q N_1 \qquad 1a$$

$$\frac{1}{N_2}\frac{dN_2}{dt} = \mu_{21}R_1 + \mu_{22}R_2 - m - m_q N_2 \qquad 1b$$

$$\frac{dR_1}{dt} = a(s_1 - R_1) - V_{11}N_1R_1 - V_{21}N_2R_1 \qquad 1c$$

$$\frac{dR_2}{dt} = a(s_2 - R_2) - V_{12}N_1R_2 - V_{22}N_2R_2. \qquad 1d$$

Here V_{ij} are consumption rates, reflecting the yield coefficients $Y_{ij} = \mu_{ij}/V_{ij}$. Density-dependent mortality for species i with density N_i is modeled as $m_{qi}{N_i}^x$, where $x > 1$. For simplicity, we use quadratic mortality ($x = 2$) in the main text. We also assume equal mortality rates (m) and quadratic mortality constants (m_q), though species-specific values are considered in Supplementary Material.

Without density-dependent mortality ($m_q = 0$), coexistence requires each species to be

competitively superior on one limiting resource, represented by intersecting ZNGIs (zero net growth isoclines) (Ryabov & Blasius 2011; McPeek 2014; Kleinhesselink & Adler 2015; Letten *et al.* 2017) (Fig. 1b). Introducing density-dependent mortality does not alter invasion criteria—resource levels must still lie above a species' invasion ZNGI where $N_i = 0$—but shifts equilibrium resource levels, which now depend on species densities and thus on supply rates. The new equilibrium conditions, denoted by $\hat{\blacksquare}$'s, are:

$$\mu_{11}\hat{R}_1 + \mu_{12}\hat{R}_2 = m + m_q\hat{N}_1 \qquad 2a$$

$$\mu_{21}\hat{R}_1 + \mu_{22}\hat{R}_2 = m + m_q\hat{N}_2. \qquad 2b$$

Unlike invasion ZNGIs, these equilibrium ZNGIs vary with biomass and elevate equilibrium resource levels (Fig. S2). As supply increases, so do population densities and thus mortality, raising resource levels. Competitive species benefit from increased growth but also suffer higher mortality, while weaker competitors, at lower densities, experience less mortality. This asymmetry broadens the coexistence domain beyond what is possible under pure resource competition (Leibold 1998; McPeek 2019).

We quantitatively analyze the impact of density-dependent mortality on the boundaries between competitive exclusion and coexistence regions using mutual invasibility analysis (Chesson 2000) (Fig. 1c) (see Supplementary Material). Density-dependent mortality significantly widens the range of resource supply rates conducive to species coexistence, resulting in nonlinear boundaries between competitive exclusion and coexistence regions (Fig. 1c). The lower boundary of the coexistence zone curves downward compared to the curve of $m_q = 0$. This indicates that under conditions where species 1 dominates the community, the density-dependent effect enables species 2 to invade at a lower supply rate of resource 2.

Because species 1 cannot deplete resources to the level at its invasion ZNGI ($\mu_{11}R_1 + \mu_{12}R_2 = m$) but instead to the higher level of its equilibrium ZNGI $\mu_{11}\hat{R}_1 + \mu_{12}\hat{R}_2 = m + m_q\hat{N}_1$ due to density-dependent mortality. The same principle applies to the upper boundary of the coexistence zone when species 1 can invade a community with the resident species 2.

In general, a larger m_q results in a larger coexistence zone, indicating that stronger density-dependent mortality promotes species coexistence across an expanded range of resource supply rates (Fig. 1c). Box 1 summarizes the four possible competitive outcomes.

Density-dependent mortality reduces the likelihood of priority effects

Notably, density-dependent mortality allows coexistence even when two generalist species would otherwise exhibit a priority effect (Chesson 2000; Fukami 2015; Grainger *et al.* 2019). In Fig. 1d-f, we selected consumption rates for the two species where each species consumes more of its less preferred resource ($\frac{V_{12}}{V_{11}} > \frac{V_{22}}{V_{21}}$), preventing coexistence and resulting in the first-come-first-survive scenario. The striped area on the resource plane in Fig. 1e represents where priority effects occur: the species that initially establishes itself in the community excludes the other. Without density-dependent mortality, this region expands linearly with resource supply above the coexistence point, with no intersection of the boundaries (Fig. 1e). In contrast, with density-dependent mortality, the invasion boundary for species 1 intersects with that of species 2 at sufficiently high resource supply levels (Fig. 1f). Thus, when the resource supply is low, a priority effect remains, but at sufficiently high supply, the species coexist due to increased density-dependent mortality for both species. This finding suggests that the magnitude of resource supply is crucial in determining the outcome of species competition as well as the ratio of resource supplies.

2.2 Three species and two resources

We next examine how density-dependent mortality can expand not only the domain of coexistence but also increase the total number of coexisting species. To do so, we consider a food web with three species and two substitutable resources, with two generalist species (species 1 and 2) with advantages on different resources, and one generalist species (species 3) having intermediate advantages on both resources. Without density-dependent mortality, the system exhibits two distinct regions of pairwise coexistence. As in the above example, density-dependent mortality expands the coexistence regions by bending the invasion boundaries (Fig. 1g-i). In this case, the two coexistence zones may overlap at high resource supply rates, leading to coexistence of all three species (Fig. 1i).

2.3 The diamond food web: Two species, one predator, and one resource

We next demonstrate how density-dependent mortality promotes species coexistence in a different classic system: the "diamond" food web with two species N_i competing for one resource R and consumed by a common predator P (apparent competition (Holt 1977))as:

$$\frac{1}{P}\frac{dP}{dt} = f_1N_1 + f_2N_2 - m_p \qquad 3a$$

$$\frac{1}{N_1}\frac{dN_1}{dt} = \mu_1R - m - g_1P - m_qN_1 \qquad 3b$$

$$\frac{1}{N_2}\frac{dN_2}{dt} = \mu_2R - m - g_2P - m_qN_2 \qquad 3c$$

$$\frac{dR}{dt} = a(s - R) - V_1N_1R - V_2N_2R, \qquad 3d$$

where f_i is the growth rate of the predator from consumption of species i at predation rate g_i, and where m_p denotes the mortality rate of the predator. As in the case of resource

competition, to coexist, in the absence of density-dependent mortality the two species' ZNGIs must intersect on the predator-resource plane (Fig. 1k). The stability of this equilibrium depends on the condition that the species with superior resource-competitive capabilities is more poorly defended against the predator, while the worse resource competitor is better-defended against the predator (Leibold 1996). Here, we assume that species 1 is the better resource competitor and species 2 is better defended against the predator, i.e., $\mu_1 > \mu_2, g_1 > g_2$.

With density-dependent mortality, the two critical resource supply concentrations are given by:

$$s_{21} = \frac{(g_1 - g_2)m - m_q \frac{m_p g_2}{f_1}}{g_1\mu_2 - g_2\mu_1}\left(1 + \frac{V_1 m_p}{a f_1}\right), \quad 4$$

and

$$s_{12} = \frac{(g_1 - g_2)m + m_q \frac{m_p g_1}{f_2}}{g_1\mu_2 - g_2\mu_1}\left(1 + \frac{V_2 m_p}{a f_2}\right). \quad 5$$

where s_{ij} denotes the threshold of the supply rate for species i invading species j (Supplementary Material). Increasing m_q increases the interval between the two invasion points (s_{21}, s_{12}), promoting coexistence. We note that the invasion point of species 2 is still bounded by its minimum supply, which is determined by the intercept of its ZNGI and the supply axis. Unlike the previous cases (Fig. 1a-i), further increasing resource supply does not necessarily result in coexistence, as it ultimately goes beyond the coexistence interval, favoring the superior apparent competitor, species 2 (Fig. 1l). This distinction will drive the shift of the community composition towards species with higher predator resistance.

Note that the case of no density-dependent mortality ($m_q = 0$) can be considered a special case of these more general equations (Supplementary Material). The four possible competitive

outcomes are summarized in Box 1 and depicted in Fig. 1i-l.

3. Control formulas for complex systems

We have shown that density-dependent effects promote species coexistence and can enable the number of coexisting species to exceed the number of limiting factors in simple systems. However, the graphical analysis used in such cases is difficult to quantitatively extend to communities with more than a few species.

To gain traction in studying complex systems where many details of the food web remain unknown, we consider a subset of the community in which coexisting species share either a common resource or a common predator, which we refer to here as a 'bottom-up' or a 'top-down' or guild. This approach aligns with a common and ecologically realistic strategy of analyzing food-web modules—simplified sub-networks where species interactions are governed by basic trophic relationships, such as resource consumption and predation (Holt 1997)—while still allowing considerable complexity in the rest of the food web. For example, tropical forests, which harbor high plant diversity competing for similar resources (Gentry 1988), and marine phytoplankton, which compete for a limited set of inorganic nutrients (Hutchinson 1961), both exemplify bottom-up guilds. Top-down control is evident in freshwater lakes, where invertebrate and vertebrate predators structure distinct prey assemblages (Werner & McPeek 1994). Similarly, microorganisms of comparable size often share predators due to size-based predation (Clauset & Erwin 2008; Ward *et al.* 2012; Follett *et al.* 2022).

We thus consider two guilds: (1) a bottom-up guild, in which multiple species compete for

a single shared resource, while their interactions with higher-level predators remain unspecified (Fig. 2a); and (2) a top-down guild, in which multiple species are preyed upon by a single shared predator, with unspecified details of their resource use (Fig. 2b). Considering these guilds, each with a single shared limiting factor, permits analytical treatment that would be intractable in fully specified complex networks.

We next develop analytical expressions to characterize coexistence patterns of these guilds. We derive a control formula in a general form that applies to both the bottom-up and top-down guilds that captures coexistence dynamics (Section 3.1), for which density-dependent mortality is one key factor. We present the specifics of the bottom-up formula (Section 3.2), noting that the corresponding specifics of the top-down guild follows a similar derivation and structure (Box 2). We then use the bottom-up formula to provide a mechanistic explanation for two commonly observed patterns in productivity–diversity relationships, and the factors that determine whether one or the other should emerge (Section 4).

3.1 The general control formula

We derive a general formula for the abundance of species applicable to both guild types (see Supplementary Material), before detailing the specific expression for the bottom-up guild (below) and the top-down guild (Box 2, Supplementary Material). The derivation assumes that equilibrium has been reached for the given guild. The resulting steady-state density $\widehat{N}_i$ of species i is:

$$\widehat{N}_i = \overline{N} + \frac{(G_i - \bar{G})}{m_q}$$

$$= [\text{average equilibrium density}] + \frac{[\text{ growth advantage/disadvantage of species } i]}{[\text{strength of density-dependent mortality}]} \quad 6$$

The quantity $\bar{N}$ is an appropriately weighted average density, set by either the predator or the resource (details below). Thus, $\bar{N}$ is set by the species of the guild that can coexist (i.e., have a positive steady-state density) at equilibrium, which may be the complete set or a subset of all possible species. G_i is the net growth rate of species i, which we define as the net growth excluding the density-dependent term (i.e., $G_i = \sum_h \mu_{ih} R_h - m - \sum_h g_{hi} P_h$). Finally, $\bar{G}$ is the weighted average growth rate of the sustained species in the community, with a specific form determined by the guild type. Note that we here assume a static (non-oscillatory) equilibrium state, although oscillatory equilibria can be treated similarly by averaging species densities over full cycles.

Equation 6 thus explains the equilibrium density of a species as determined by three components. The first component, the average density of the community ($\bar{N}$) is intrinsically linked to the shared limiting factor (resource or predator) defined by the guild type. The second component is the discrepancy between the net growth rate (G_i) of the focal species and the weighted community average net growth rate. When the value of the focal species' G_i surpasses that of the community average ($\bar{G}$), it represents a relative competitive advantage that elevates the species' abundance above the average. The third component is the strength of density-dependent mortality ($\frac{1}{m_q}$), which modulates the impact of the second component. When density-dependent mortality is negligible ($m_q = 0$), all coexisting species must have the same net growth rate ($G_i = 0$). In contrast, when density-dependent mortality is sufficiently large, species with net growth rates lower than the community average may be sustained, allowing for larger diversity of the guild at equilibrium.

3.2 The specific control formula for the bottom-up guild

In a bottom-up guild, multiple consumer species compete for and are limited by a single shared resource and unspecified predators, given by (Fig.3a):

$$\frac{1}{N_i}\frac{dN_i}{dt} = \mu_i R - m - \sum_h g_{hi} P_h - m_q N_i \qquad 7a$$

$$\frac{dR}{dt} = a(s - R) - \sum_i V_i N_i R. \qquad 7b$$

with parameters as defined above (Eqn. 1). The specific form of the control formula Eq. (6) for the bottom-up guild is given by

$$\widehat{N}_i = \frac{a(s-\hat{R})}{\sum_j^n V_j \hat{R}} + \frac{1}{m_q}\left(G_i - \frac{\sum_j^n V_j G_j}{\sum_j^n V_j}\right) \qquad 8$$

where the average density is $\overline{N} = \frac{a(s-\hat{R})}{\sum_j^n V_j \hat{R}} = \frac{\sum_j^n V_j \widehat{N}_j}{\sum_j^n V_j}$, which is the resource supply rate ($a(s - \hat{R})$) divided by the total consumption rate by all sustained species ($\sum_j^n V_j \hat{R}$). The effects of predation are incorporated into the effective resource level $\hat{R}$, because predation reduces prey densities and thereby indirectly influences the equilibrium resource concentration. (This relationship is reflected in the equilibrium condition derived by setting Eqn. 7a to zero, yielding $\hat{R} = \frac{1}{\mu_i}(m + \sum_h g_{hi}\hat{P}_h + m_q \widehat{N}_i)$.) In this framework, the average community growth rate is weighted by each species' resource consumption rate $\bar{G} = \frac{\sum_j^n V_j G_j}{\sum_j^n V_j}$, where $G_j = \mu_j R - m - \sum_h g_{hk} P_h$. Thus, Eqn. 8 reveals a trade-off between species density and diversity (which also applies to the top-down guild). As the strength of density-dependent mortality (m_q) increases, allowing more species to coexist, the average species density declines.

The utility of this bottom-up control formula is that it allows us to link resource supply, traits, and species abundances (and thus diversity) mechanistically, so that we can understand and potentially predict diversity patterns as a function of resource supply. For example, the

bottom-up control formula (Eqn. 8) can be used to derive the minimum resource supply rate required to sustain a particular species. For species i, the threshold supply rate corresponds to the condition under which its equilibrium density becomes positive, resulting in the inequality:

$$s > \hat{R} + \frac{1}{am_q} \sum_{j=1}^{i-1} V_j \left(G_j - G_i \right) \hat{R} \qquad 9$$

This expression defines the minimum supply rate necessary for species i to persist, given the presence of other coexisting species with higher net growth rates. The summation term captures the cumulative effect of fitness differences weighted by resource uptake rates between species i and other species that coexist at lower supply rates. If the species with the lowest net growth rate (G) can maintain a positive density at equilibrium (Eqn. 6), all other species with higher G values can also persist. This provides a tractable criterion for quantifying coexistence and diversity. Moreover, since resource supply sets productivity in an ecosystem, we can use this framework to analyze how species' net growth rates vary with resource supply to gain insight into the relationship between productivity and diversity.

4. Mechanistic explanations for distinct productivity-diversity relationships

Our formulation (Eqn. 8 and 9) links resource supply rate, which governs the productivity of the ecosystem, to species richness and diversity. We next explore how this framework provides a mechanistic basis for explaining distinct, yet commonly observed productivity–diversity patterns (PDRs).

4.1 Increasing productivity-diversity relationship

We begin by analyzing a bottom-up guild composed of multiple species competing for a shared limiting resource. Critically, we assume that predation is negligible, which can be an

appropriate assumption for phytoplankton communities competing for scarce nutrients with little grazing pressure in oligotrophic systems (Reynolds 1984) or heterotrophic microbial communities in the deep ocean, consuming organic substrates below the more productive sunlit zone (Moeller *et al.* 2019).

To illustrate the dynamics clearly, we consider a species pool in which species are ranked in descending order of their intrinsic growth rates, i.e., $\mu_1 > \mu_2 > \cdots > \mu_i$. Thus, the species with the lowest growth rate μ must then also have the lowest net growth rate ($G_i = \mu_i R - m$), and so if this species can subsist in the environment, then all potential species in the set can subsist. As the supply concentration s increases from a low level (e.g., $s = 0$), the first species able to invade is the one with the highest intrinsic growth rate (also highest G). When density-dependent mortality is also negligible (e.g., $m_q = 0$), Eqn. 9 shows that the denominator diverges and any differences in the net growth rates G are effectively amplified, implying that no finite supply rate can support the persistence of an inferior competitor. From the perspective of resource competition, the first species can deplete the resource to its R^*, which is the lowest $R*$ of the community, and does not increase with the supply rate. Thus, it prevents the other species from invading. In contrast, with density-dependent mortality ($m_q > 0$), the equilibrium resource concentration increases with the supply rate (Supplementary Material and Fig.S1 and Fig. S3):

$$\frac{d\hat{R}}{ds} > 0. \qquad 10$$

As a result, the minimum $R*s$ of other species can be reached, achieving coexistence between multiple species. From Eqn. 9, the supply rate required for coexistence of a second species increases with the difference in growth rates between the two species and decreases with the

strength of density dependence (m_q), again highlighting the role of density dependence in promoting coexistence by mitigating competitive exclusion.

Thus, as the resource supply rate increases, additional species with progressively lower intrinsic growth rates can invade. Resident species are not excluded because the net growth rate $G_i = \mu_i R - m$ is a monotonically increasing function of the equilibrium resource concentration $\hat{R}$, indicated by

$$\frac{dG_i}{ds} = \mu_i \frac{d\hat{R}}{ds} > 0 \qquad 11$$

and so G_i increases with the supply rate. This process generates a monotonically increasing PDR (Fig. 4).

More generally, our framework thus indicates that an increasing PDR is expected whenever the net growth rate G does not decrease with respect to increased productivity for the majority of species if apparent competition is negligible. That being said, predation itself needs not be negligible, because we also predict an increasing PDR in systems where predation is sufficiently specialized on prey such that it minimizes apparent competition (Fig. 4a).

4.2 Unimodal productivity-diversity relationship

To clearly illustrate the emergence of a qualitatively different PDR, we again consider the diamond food web structure, a simple but ecologically relevant case where prey species share a single resource and a common predator (Section 2.3) (Levin 1970; Holt *et al.* 1994; Leibold 1996). In essence, in contrast to the bottom-up guild, here, apparent competition from predation is not negligible. As above (Section 2.3), we assume a trade-off between intrinsic growth rate and vulnerability to predation among the species pool, reflecting a spectrum of evolutionary strategies ranging from efficient resource exploiters (high μ, high g) to predator-resistant

species (low μ, low g). For clarity, we consider species as ordered by decreasing intrinsic growth rates ($\mu_i > \mu_{i+1} > \cdots > \mu_k$), so that pairwise coexistence is possible when the ratio ($\frac{\mu_i}{g_i}$) increases across species (i.e., $\frac{\mu_i}{g_i} < \cdots < \frac{\mu_k}{g_k}$) (Leibold 1996).

In the diamond food web, in contrast to the above case, the net growth rate $G_i = \mu_i R - m - g_i P$ is no longer a monotonic function of the resource supply rate. The derivative of G_i with respect to s takes the form

$$\frac{dG_i}{ds} = \left(\mu_i - g_i \frac{\sum_j f_j \mu_j}{\sum_j f_j g_j}\right) \cdot \frac{d\hat{R}}{ds} \qquad 12$$

Eqn. 12 indicates that G exhibits variable responses to changes in the supply rate s and species diversity (Supplementary Material).

As above, increasing the supply rate increases the resource concentration, allowing more and more species to invade. However, the term $\mu_i - g_i \frac{\sum_j f_j \mu_j}{\sum_j f_j g_j}$ is a decreasing function in terms of diversity when more species with sequentially smaller μ and g than the ith species invade (Supplementary Material). Consequently, as the resource supply rate continues to increase, allowing more predation-resistant species to invade, species optimized for fast growth, but not for predation resistance, go extinct as their Gs decrease to negative values. This pattern occurs sequentially along the supply gradient, ultimately resulting in a unimodal PDR (Fig. 3c,d). Thus, our framework indicates that when apparent competition from shared predation is sufficiently large in the community, a peak in diversity along the productivity spectrum is expected.

4.3 The emergence of multiple PDRs within one framework

Thus far, we have used the control formula to mechanistically explain the emergence of both increasing and unimodal PDRs. The main control that determines whether one or the other emerges lies in the details of the community structure, and specifically, whether or not apparent competition from shared predation is negligible. A structural shift between the two PDRs could thus result from ecological or evolutionary changes that lead to predator extinction, colonization, or increasing predator specialization. This generates a testable hypothesis: in systems where predation pressure declines (e.g., through predator loss or niche partitioning), diversity should increase monotonically with productivity. We are not aware of any experimental study that directly tests this prediction, but this hypothesis could be tested with ecosystem manipulation experiments where predators are added or removed systematically.

More generally, our framework indicates that the strength of apparent competition from shared predation, not solely its presence or absence, has a strong control on the emergent PDR. To illustrate the transition from the increasing to the unimodal PDR as a function of this control, we simulate ecosystems where species compete for a single limiting resource while varying the number of predator species (Fig. 4a). We assume that each predator targets a distinct group of prey (Fig. S5), with adjacent predators sometimes overlapping in prey species. When the number of predators is small (<10 in our simulations), apparent competition from shared predation is strong, and the unimodal productivity–diversity curve emerges (Fig.4a). As the number of predators increases and their diets become more specialized, apparent competition is reduced, and the curve shifts toward an increasing pattern, eventually converging to the pattern seen in bottom-up guilds where predation is entirely negligible. Thus, species-specific predation (NOP = 100) also generates an increasing PDR. Stronger density dependent mortality

modulates the quantification of this curve and generally promotes higher species diversity at lower levels of productivity (Fig. S6).

4.4 Insights into observed patterns

We next analyze two datasets that report contrasting PDRs in plant communities (Fig. 4, (Adler *et al.* 2011; Fraser *et al.* 2015)). After pooling all data together across sites, with total biomass used as a proxy for productivity, we apply a standardized and consistent statistical framework to each dataset (Supplementary Material) to find that the data from Adler et al. 2011 supports a significantly increasing PDR, whereas the data from Fraser et al. 2015 exhibits a unimodal (hump-shaped) relationship (Fig. 4bc). However, despite these differences in statistical fit, the patterns of the two datasets seem visually indistinguishable, highlighting the difficulty of discerning the PDR based on empirical data alone. Additionally, both original studies found that within-site regressions reveal a diversity of patterns, which we also recovered (Fig. 4bc), including increasing and unimodal (concave-down) patterns as well as decreasing and concave-up patterns, and that many sites indicated no significant relationship.

Our framework can be used to provide insight into these widely varying observed PDRs (Fig. 4). Our simulations show that a variety of PDRs could effectively be observed if sampling is limited to a portion of the productivity gradient (Fig. 4a). For example, a decreasing relationship would be inferred if only the “right-hand-side” component of the unimodal curve were observed. This sub-sampling could explain much of the within-site PDR variability. Although we did not generate the concave-down relationship, it may emerge from multiple unidmoal PDRs occuring sequentially along the supply axis. Generally, our simulations suggest

that: 1) unimodal PDRs are most likely to emerge if a wide range of productivity levels are sampled, 2) increasing PDRs may be more likely to be observed at low productivity levels (as the "left-hand-side" components of a unimodal curve in addition to actual increasing PDR across the entire productivity domain), and 3) declining PDRs are more likely to be observed at relatively high productivity levels. Again, we posit that differences in the strength of apparent competition from shared predation is a main control on the emergent PDRs.

5. Outlook

We have provided a thorough, quantitative analysis of how density-dependent mortality impacts community structure. Building on resource competition theory, density-dependent mortality bends the boundaries between competitive exclusion and coexistence, expanding coexistence zones along resource gradients. Extending the analysis beyond graphical analysis of a few species, we derived a control formula for two types of guilds embedded within complex ecosystems with any number of species, where species compete for resources (bottom-up) or share predators (top-down). The control formula predicts species abundance distributions, with the abundance of a given species attributed to three factors: the average biomass set by the resource or predator, its deviation from the community-averaged net growth rate, and the strength of density-dependent mortality.

The control formula, for which density-dependent mortality is a key aspect, allows for a unifying explanation for either an increasing or a unimodal diversity–productivity curve, depending on the underlying food web details. When predation is negligible or highly specialized, increasing resource supply allows species with lower growth rates to persist,

resulting in a monotonic increase in species richness with productivity. In contrast, when density is additionally constrained by shared predation (generating apparent competition), diversity peaks at intermediate productivity levels. Previously, heterogeneity in space or in time was invoked to explain such relationships, with each potential explanation only accounting for one pattern (Abrams 1988; Leibold 1996).

More generally, our results contribute to the necessary work of extending theoretical analysis of ecosystem structure to complex ecosystems, such as microbial communities with thousands of species. The control formula for guilds provides a tractable way forward for understanding the abundance and thus the coexistence of many species (or species-like entities) as a function of tangible quantities that can be related to traits, rather than phenomenological interaction coefficients used by the Lotka-Volterra equations. In this way, our mechanistic framework paves the way towards predictive capability in complex ecosystems.

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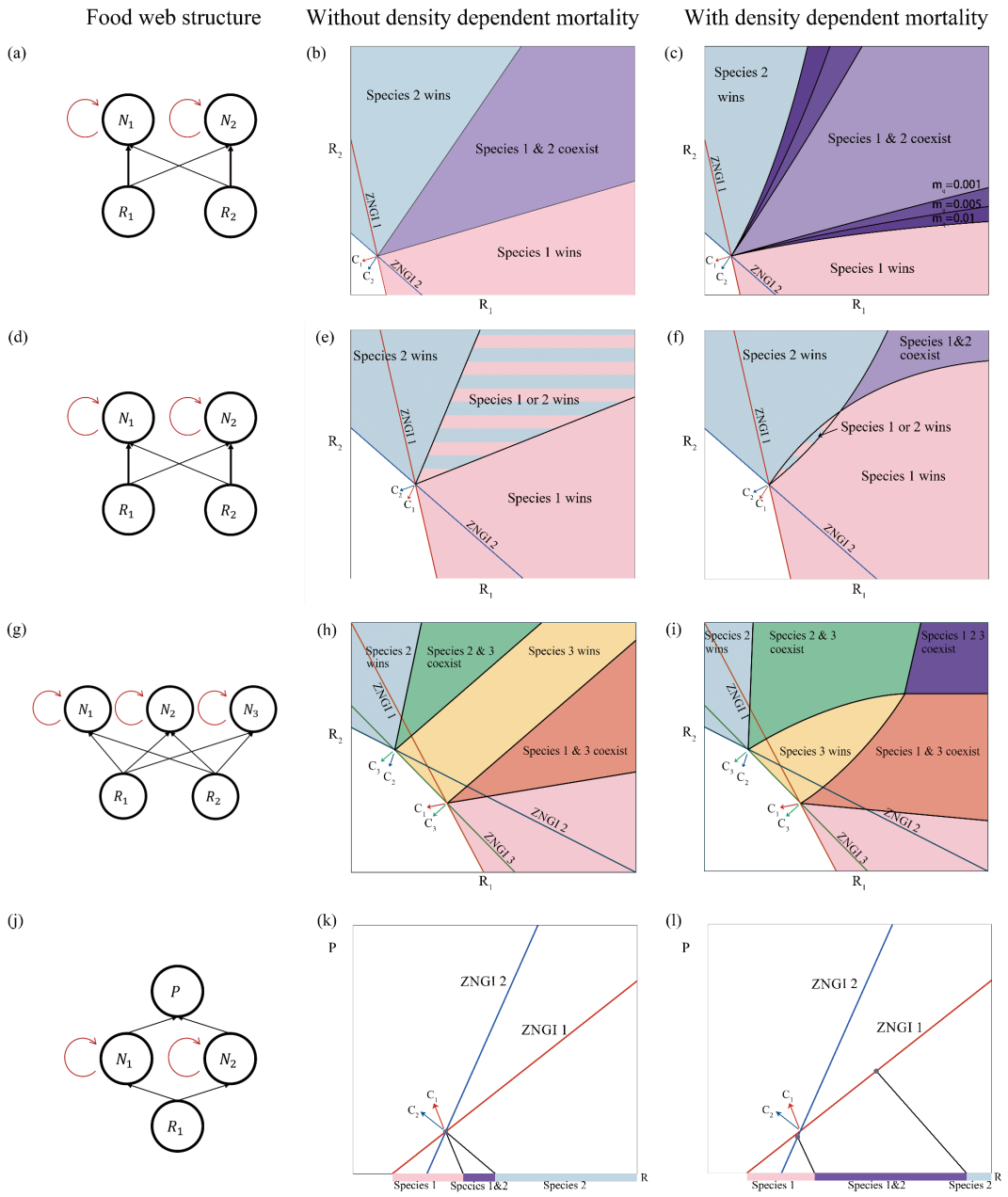
Food web structure
Without density dependent mortality
With density dependent mortality
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
Species 2 wins
Species 1 & 2 coexist
Species 1 wins
ZNGI 1
ZNGI 2
Species 2 wins
Species 1 & 2 coexist
Species 1 wins
Species 1 or 2 wins
Species 1&2 coexist
Species 2 & 3 coexist
Species 3 wins
Species 1 & 3 coexist
Species 1 2 3 coexist
ZNGI 3
P
Species 1
Species 1&2
Species 2
R

Figure 1. : Illustration of the range of resource supply rates for the species coexistence with/without the density-dependent effect. The impact vectors of species on resources are denoted by c_1, c_2, c_3. (a), (d), (g), (j). The food web structures. (b). The two generalists can coexist when $m_q = 0$; (d). Increasing m_q expands the range of resource supply rates for species coexistence. The model parameters are $\mu_{11} = 1.0, \mu_{21} = 0.2, \mu_{12} = 0.5, \mu_{22} = 0.5, V_{11} = 3.3, V_{21} = 0.67, V_{12} = 1.67, V_{22} = 1.67, m = 0.1, a = 1$; (e). The two generalists cannot coexist when $m_q = 0$ because their impact vectors indicate a priority effect; (f). The effect of density dependence facilitates coexistence at higher supply rates. For the supply rates vector falls in the striped zone, the priority effect emerges. The model parameters are $\mu_{11} = 1.0, \mu_{21} = 0.2, \mu_{12} = 0.5, \mu_{22} = 0.5, V_{11} = 1.1, V_{21} = 1.8, V_{12} = 2.2, V_{22} = 0.6, m = 0.1, a = 1$. (h). When $m_q = 0$, at most two species can coexist in the supply rate space. The outcome of species interaction depends on where the vector of resource productivities falls.; (i). When $m_q = 0.01$, the two pairwise coexistence zones overlap, indicating an area where three species can coexist. The model parameters are $\mathrm{a} = 1, \mu_{11} = 0.27, \mu_{22} = 0.24, \mu_{13} = 0.15, \mu_{23} = 0.15, V_{11} = 0.9, V_{22} = 0.8, V_{12} = 0.5, V_{22} = 0.5, m = 0.1, a = 1$. (k-l). In the diamond food web, two species can coexist at a larger range of supply rates with increase of m_q; (k).$m_q = 0$; (l). $m_q = 0.01$; The boundaries are given by Eqns. 4 and 5. The model parameters are $\mu_1 = 2.8, \mu_2 = 1.2, V_1 = 4.2, V_2 = 1.8, g_1 = 8.7, g_2 = 1.725, f_1 = 5.8, f_2 = 1.15, m = 0.1, m_p = 0.1, a = 1$.

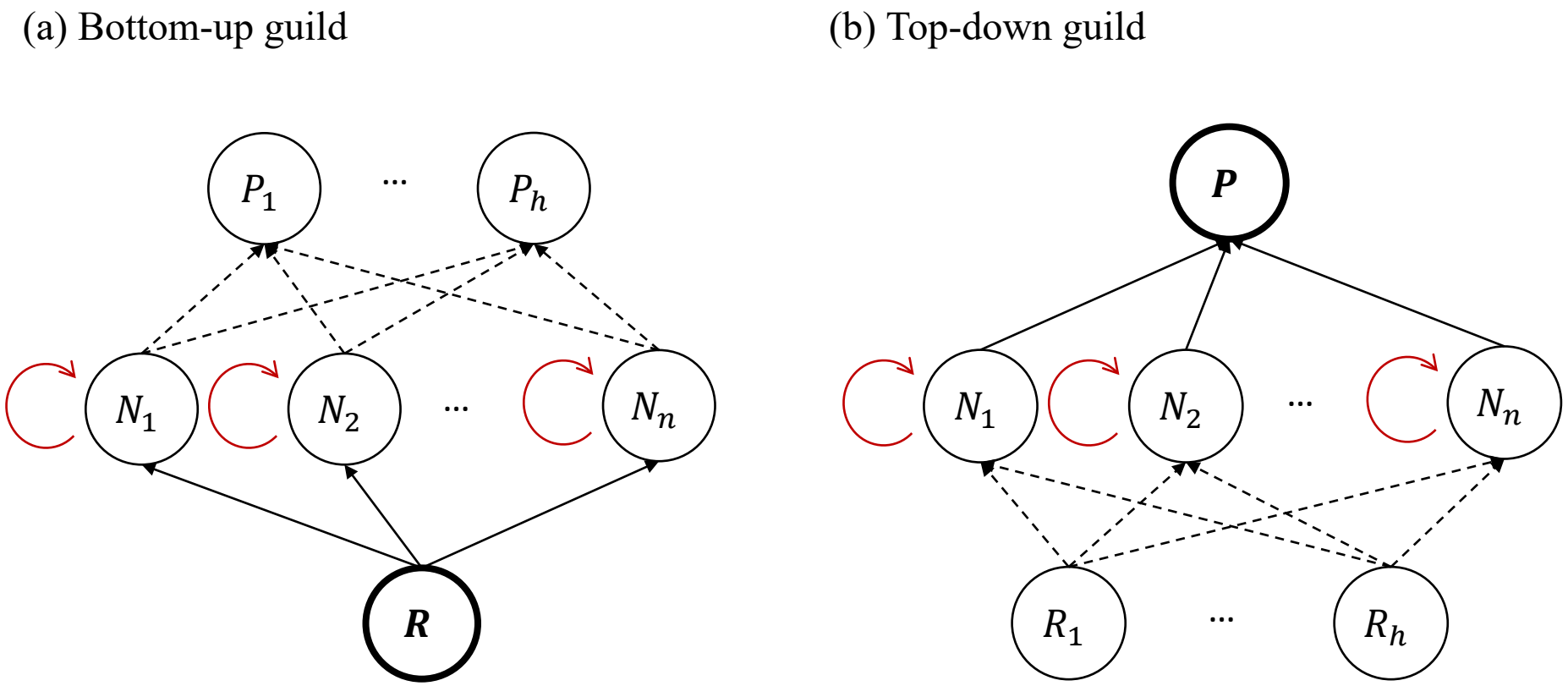

Figure 2: Two types of guilds illustrating species interactions within and between trophic levels. The negative density dependence is denoted by the red arrows. (a). The bottom-up guild assumes that consumer species are mainly limited by food availability of one common resource; (b) The top-down guild assumes that consumer species are restricted by the common predator.

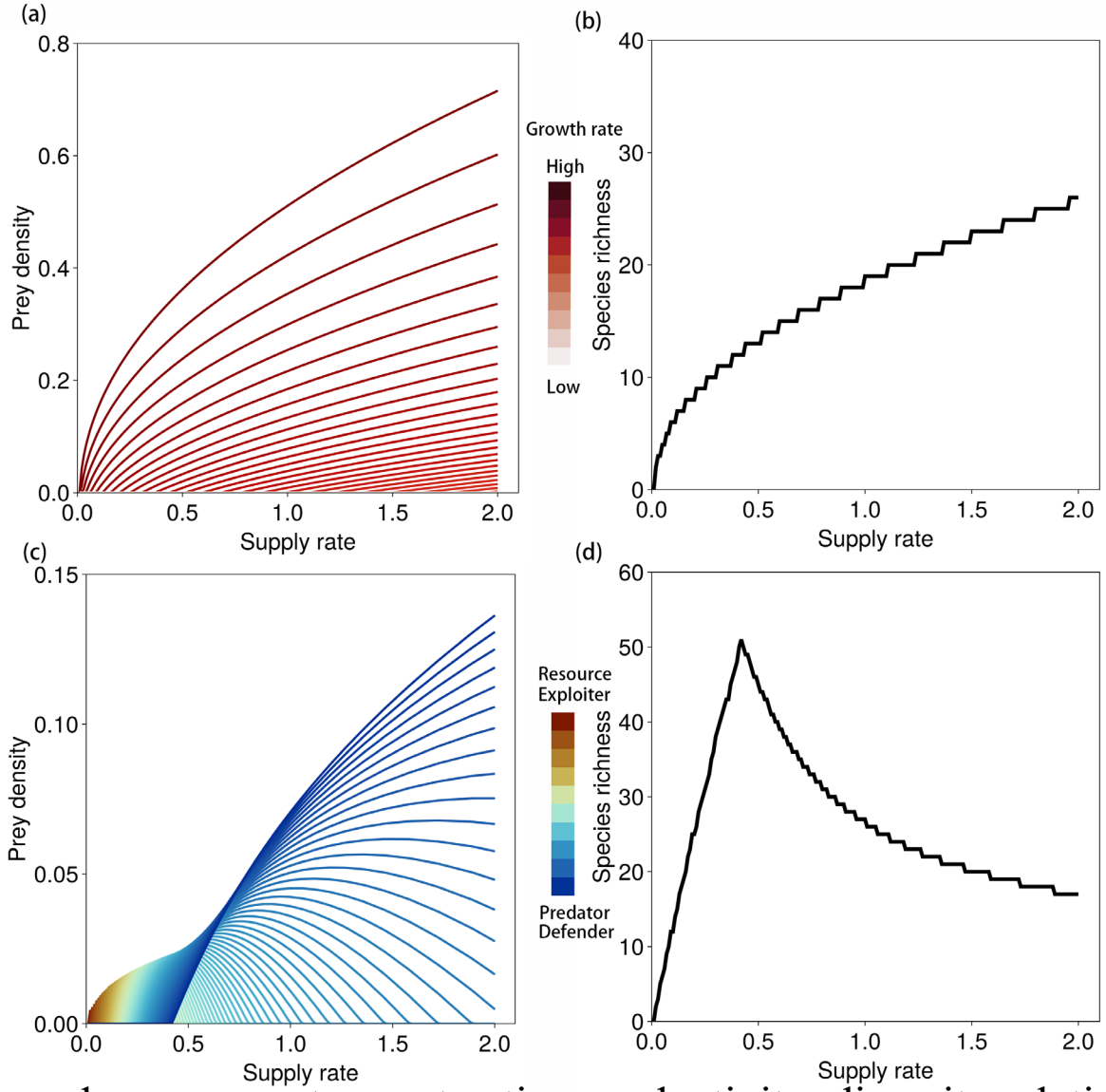

Figure 3: Negative density dependence generates contrasting productivity–diversity relationships. (a) Simulation of a bottom-up guild with 100 species ranked by growth rates (color gradient). (b) In the presence of density-dependent mortality, species richness increases with resource supply. (c) Simulation of a diamond food web with 100 species, sharing a common predator and resource. Species are ranked by growth and predation rates. (d) Under density-dependent mortality, the resulting productivity–diversity relationship becomes unimodal.

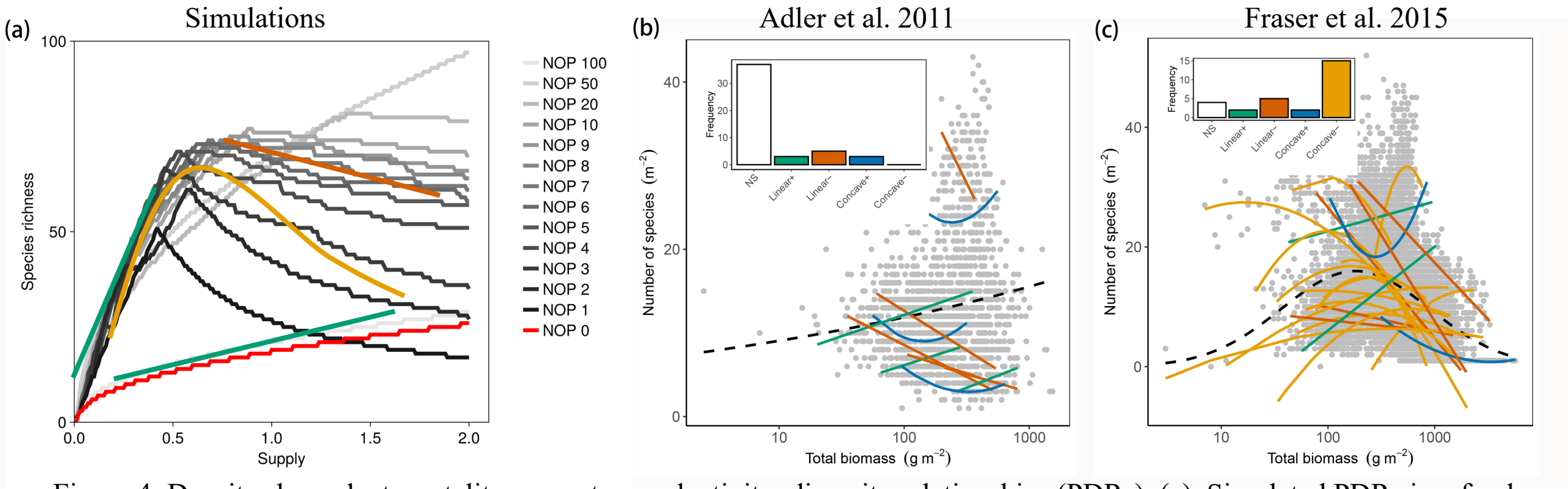

Figure 4: Density-dependent mortality generates productivity–diversity relationships (PDRs). (a). Simulated PDRs in a food web with 100 prey species and varying number of predators (NOP=0,…, 100). Different PDR shapes emerge at different ranges of resource supply rates (indicated by colored lines). (b); (c). Empirical PDRs compiled from Adler et al. 2011 and Fraser et al. 2015 (see Supplementary Material). Solid lines show within-site regressions; dashed lines indicate regressions pooled across sites. Inset panels show the distribution of observed PDR types: NS = non-significant, Linear+ = positive linear, Linear− = negative linear, Concave+ = anti-unimodal, and Concave− = unimodal relationships.

Text box 1:

In a food web with two species competing for two nutritionally substitutable resources, density-dependent mortality affects the four regions of the resource plane as follows (Fig. 1a-c):

- **Region of no species**: This zone is bounded by the invasion ZNGIs of the two species and two resource axes. In this zone, the supply of both resources is severely limited and cannot support the persistence of either species. This zone is not changed when incorporating density-dependent mortality because the minimum requirement of resources is not impacted: the invasion ZNGIs remain constant as Eqn. 1a-b do not depend on m_q when $N_i = 0$.

- **Regions of competitive exclusion**: In these regions, resource 1 (or 2) is sufficiently supplied, which allows species 1 (or 2) to maintain its presence. In contrast, the limited supply of resource 2 (or 1) hinders the survival of species 2 (or 1), resulting in its exclusion. The presence of density-dependent mortality narrows this zone and allows species 2 (or 1) to eventually persist with the increase of the supply concentration of resource 2 (or 1).

- **Region of coexistence**: This region is bounded by two boundaries characterized by adequate resource supply levels for both resources. Consequently, it creates an environment where both species can coexist. Density-dependent mortality significantly expands this zone (Fig. 1c).

In a food web with two species N_i competing for one resource R and consumed by a common predator P, density-dependent mortality affects the four regions of the resource plane as follows (Fig. 1j-l):

- **Region of no species**: When $s < R_1^* = \frac{m}{\mu_1}$, resource supply is insufficient to meet the minimum requirement for either species, even for the best resource exploiter. No species can persist in this range of resource supply rate. Incorporating density-dependent mortality does not change this threshold.

- **Region of species 1 winning**: When $R_1^* < s < s_{21}$, species 1 can persist, but not species 2. Specifically, in the range of $R_1^* < s < R_2^* = \frac{m}{\mu_2}$, species 2 cannot persist because the resource supply concentration is below its minimum requirement. When $R_2^* \leq s < s_{21}$, species 2 is excluded by competition with species 1. Density-dependent mortality decreases s_{21} (Eqn. 4), which allows species 2 to invade at a lower resource supply compared to the case of no density-dependent mortality.

- **Region of coexistence**: When $s_{21} < s < s_{12}$, both species can coexist. The effect of density-dependent mortality expands the coexistence region through increasing s_{12} and decreasing s_{21} with increasing m_q (Fig. 1k,l).

- **Region of species 2 winning**: In the last region where $s > s_{12}$, only species 2 can survive. Increasing resource supply raises the total density of consumer species, resulting in an increase in the density of the shared predator. This apparent competition leads to the exclusion of species 1.

Text box 2:

The control formula for top-down trophic guilds

In a top-down trophic guild, all species are preyed upon and largely controlled by a common predator, with unspecified resources, given by (Fig. 2b):

$$\frac{1}{P}\frac{dP}{dt} = \sum_i f_i N_i - m_p$$

$$\frac{1}{N_i}\frac{dN_i}{dt} = \sum_h \mu_{ih} R_h - g_i P - m - m_q N_i.$$

In this case, the explicit form of the control formula Eq. (7) is given by

$$\widehat{N}_i = \frac{m_p}{\sum_j^n f_j} + \frac{1}{m_q}\left(G_i - \frac{\sum_j^n f_j G_j}{\sum_j^n f_j}\right)$$

where the average biomass density reflects the control from the predator as $\bar{N} = \frac{m_p}{\sum_j^n f_j} = \frac{\sum_j^n f_j \widehat{N}_j}{\sum_j^n f_j}$, which is the subsistence concentration of the predator, or the mean density $\widehat{N}_j$ weighted by the predation rate f_j. The average community growth rate is weighted by the predator's assimilation (consumption) rate on each species f as $\bar{G} = \frac{\sum_j^n f_j G_j}{\sum_j^n f_j}$, where $G_i = \sum_h \mu_{ih} R_h - g_i P - m$.