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To cite this version:

Guim Aguadé-Gorgorió, Ismaël Lajaaiti, Jean-françois Arnoldi, Sonia Kéfi. Unpacking sublinear growth: diversity, stability and coexistence. Oikos, 2025, 2025 (1), pp.e10980. 10.1111/oik.10980 . hal-04902736

HAL Id: hal-04902736
https://hal.umontpellier.fr/hal-04902736v1

Submitted on 21 Jan 2025

Unpacking sublinear growth: diversity, stability and coexistence

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(Dated: October 21, 2024)

ABSTRACT

How can so many species coexist in natural ecosystems remains a fundamental question in ecology. Classical models suggest that competition for space and resources should maintain the number of coexisting species far below the staggering diversity commonly found in nature. To overcome this paradox, theoretical studies have long highlighted a number of mechanisms that can favour species coexistence, from the distribution of interaction strengths between species to the shape of population growth functions. In particular, a family of mathematical models finds that, when sublinear population growth (SG) rates are coupled with competition between species, species diversity can stabilize community dynamics. This could suggest that SG may explain the stable coexistence of many species in natural ecosystems. Here we clarify why SG models do not solve the paradox of species coexistence. This is because, in the SG model, coexistence emerges from an unrealistic property, in which population per-capita growth rates tend to infinity at low abundance, preventing species from ever going extinct due to competitive exclusion. Infinite growth at low abundance can be regularized by assuming a minimal abundance threshold, below which a species goes extinct or follows non-infinite growth curves. When this is done, the SG model recovers the classical result: increasing the diversity of the species pool leads to competitive exclusion and species extinctions.

I. INTRODUCTION

Naturalists in the 19th century had already realized that species competition, encapsulated in the notion of the *survival of the fittest*, was at odds with the species diversity observed in natural ecosystems. Since species compete for space and resources, one would not expect to find the high levels of diversity that are observed in ecosystems such as coral reefs or tropical forests [1–3]. Later, Robert May proposed that large, randomly interacting communities become linearly unstable if their diversity overcomes a predictable threshold [4]. The approach considers a community at an equilibrium state with all species coexisting, and assumes that the Jacobian matrix that encodes population dynamics close to the equilibrium state –the so-called *community matrix*– can be approximated by a random matrix. Eugene Wigner had previously shown that the dominant eigenvalue of a random matrix becomes positive as the matrix size, and therefore the number of species, increases [5]. This implies that a community with more species will have a higher chance of being unstable to perturbations (see Box and [4]).

May's result studies the stability of a community assuming the existence of an equilibrium state with all species present, but cannot inform about whether the loss of linear stability is related to the extinction of some species or the unbounded growth of others (see Box and [6, 7]). More recent studies have explored the dynamics of ecological communities under the Generalized Lotka-Volterra (GLV) model. By providing an explicit description for how species populations grow or decrease, the GLV model can then predict the conditions that drive species to extinction. In this model, the abundance of a given species N_i in the presence of S other species follows (see e.g. [8])

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i} - \sum_{j \neq i}^{S} A_{ij} N_j \right) . \tag{1}$$

Here r_i is the intrinsic growth rate of species i, K_i is its carrying capacity, and the *interaction matrix* A_{ij} encodes the effect of species j on the growth rate of species i. Consistent with May's results, a fundamental property of this model is that, as the initial diversity S increases, both the proportion of coexisting species and the stability of the remaining community tend to decrease [9–12]. This theoretical prediction contrasts with the remarkable species richness observed in some natural ecosystems.

Various amendments to this result have been proposed in the literature. Among others, natural communities are not random: the distribution of interaction strengths [13–15] or the structure of ecological networks [16–18] can increase the probability that many species coexist. Such mechanisms allow communities to support a higher number of species than what would be expected if interactions strengths were random. However, they do not invert the shape of the dependency: the greater the initial species diversity, the more challenging species coexistence becomes. (see Box).

In parallel with the question of species diversity in ecosystems, by the late 1980s, researchers working on the origins of life proposed that prebiotic replicators could have evolved under so-called *parabolic* growth [19, 20]. This means that the abundance N_i of a self-replicating entity would follow sublinear growth (SG) dynamics of the form

$$\frac{dN_i}{dt} = r_i N_i^k, \tag{2}$$

with $0 < k < 1$, as opposed to the classical picture of exponential growth ($k = 1$). The sublinear growth exponent indicates the presence of replication constraints, related to the fact that entities such as oligonucleotides are often found associated in a non-replicative duplex, and can only replicate in its dissociated form [21, 22]. Later, Szathmáry and colleagues found that competition among these self-replicating entities did not drive them to extinction; instead, they coexisted stably, leading to a scenario of *survival of all* [23, 24].

Moving 20 years forward and into community ecology, a theoretical model studied the outcomes of coupling linear growth rates with super-linear death rates emerging from crowding effects [25], with the form

$$\frac{dN_i}{dt} = r_i N_i - d_i N_i^{1+k}, \tag{3}$$

with $k > 0$. Similar to the dynamics of parabolic replicators, the authors found that competition between these species did not lead to competitive exclusion. In their own words, which will be particularly interesting for the discussion presented here, the *"model seems to imply unconditional coexistence is possible. However, the population per-capita mortality rates vanish for small population densities. Hence, the observed coexistence may be artificial and 'unbiological'"* [25]. Models where growth rates scale sublinearly with population abundance have also been applied not only as variations of the GLV model of many interacting species [26], but also to describe eco-evoluationary dynamics [27] or tumor growth [28, 29].

A recent study has also used a SG model to study the dynamics of ecological communities of interacting species [30]. The work finds that a SG rate coupled with bilinear competition between species can lead to a positive relationship in which diversity increases the linear stability of a community at equilibrium [30]. In other words, under SG, more diverse communities would be more resilient to small perturbations in species abundances. In terms of coexistence, the SG model leads to a *survival of all*, suggesting that SG can prevent species from going extinct due to competitive exclusion. If this were the case, the model would offer a direct explanation for how many species can coexist despite competition [2, 3].

Yet, how does coexistence and *survival of all* emerge in this family of SG models? Here we clarify that species coexistence in a SG model emerges from an unrealistic assumption, by which population per-capita growth rates become infinite at low abundance, preventing species extinctions due to competitive exclusion. A more common assumption, as discussed below and in [30], is that population growth rates remain bounded or even become negative at low abundances [31–33]. A limit-case scenario is that of the well-established Allee effect, that assumes negative population growth at low abundance. Opposite to the divergingly large population per-capita growth rates of the SG model, the Allee effect establishes a minimal species abundance, below which factors like group protection or mate encounters become insufficient for successful population growth [30, 32, 34].

Before exploring the dynamics of the SG model, it is important to recall that linear stability and species coexistence are two different properties (see Box). The diversity-stability relation investigates whether a system with more initial species becomes more or less stable to perturbations. The diversity-coexistence relation investigates whether a system with more initial species has a smaller or larger probability to see all species surviving together [3]. In the Generalized Lotka-Volterra (GLV) model defined by Eq. 1, for example, increasing species diversity leads to two consecutive results [12]. First, it disrupts community coexistence by pushing some species to extinction [10, 12]. Second, it destabilizes species abundances, leading to chaotic fluctuations and multiple stable states [11, 12, 35]. This means that, in the GLV model, the two relations go hand in hand: diversity disrupts both species coexistence and linear stability [12]. In other models, however, the two mechanisms need not be equivalent: an increase in initial diversity could drive a community towards a more stable state (increased stability) where some species have nevertheless gone extinct (decreased coexistence).

Here we study a SG model in which species grow with a sublinear exponent, die at a linear rate and compete bilinearly with other species (see e.g. [23, 24, 30]),

$$\frac{dN_i}{dt} = r_i N_i^k - d_i N_i - N_i \sum_{j \neq i}^{S} A_{ij} N_j. \tag{4}$$

In this model, r_i is the population growth rate of species i, d_i its death rate and A_{ij} again describes the competitive effects of species j on species i. A possible scaling exponent of $k \approx 3/4$ has been recently estimated from macro-ecological data of biomass-productivity relations [30, 36]. A fundamental assumption of this model is that, while growth rates are sublinear with species abundances (N_i^k), death and competition terms are linear and bilinear respectively ($-d_i N_i$, $-N_i A_{ij} N_j$). Open questions remain regarding the factors that could explain the discrepancy between the exponents of intra- and inter-specific interactions, or else if sublinear exponents smaller than 1 could also be at play in inter-specific interactions [37–42]. Following the results of [41], below we discuss the implications of relaxing this critical assumption so that growth, death and competition are all sublinear with species abundances.

In the present work, we clarify how increasing the initial number of species affects linear stability and species coexistence in the SG model. First, we present a key particularity of the model, by which population per-capita growth rates diverge at low abundance, preventing species from going extinct (Section II). Second, we discuss the consequences of divergent growth on species coexistence (Section III). Third, we highlight that when divergent population growth dynamics are regularized to avoid infinite per-capita growth rates, increasing diversity leads to competitive exclusion in the SG model, hereby reducing species coexistence (Section IV).

II. DIVERGENT GROWTH AT LOW ABUNDANCES

A particularity of the SG model defined by Eq. 4 is that population per-capita growth rates diverge at low species abundance. This means that when the number of individuals of a given species N_i is low (due, for example, to the pressure exerted by competition with other species), their growth rate becomes extremely large, thus automatically preventing the extinction of the species. By dividing total population growth in Eq. 4 by the number of individuals, one obtains the per-capita growth rate of species i

Box 1: Diversity, stability and coexistence in ecological models

Diversity: Diversity in ecology can be measured at different scales. In community ecology diversity typically refers to the number of different species in a community. Communities are often modeled as the result of an assembly process of species migrating from a regional pool [43]. In this context, the *final diversity* of a community is then usually lower than the *initial diversity* of the species pool due to species extinctions occurring during the assembly process.

Stability: Ecological stability encompasses various meanings and can be assessed through different measures [44–48]. Most often, stability refers to the capacity of an ecosystem to maintain its unperturbed state (resistance [49]) or go back to it (resilience [50]) following a perturbation. In theoretical works, community stability is often equated to linear stability. A community state is *linearly stable* if the real part of the dominant eigenvalue of its Jacobian is negative, so that abundances of all species will relax back into their steady state after a small perturbation. Linear stability can then be a mechanism of maintenance of species coexistence, by ensuring that a coexistence state is recovered after a perturbation [51, 52]. Linear stability, however, is not a direct proxy for species coexistence: for example, a state with a single surviving competitor (competitive exclusion) or one with no surviving species (trivial equilibrium) can nevertheless be linearly stable. Also, loss of linear stability does not necessarily imply a loss of coexistence: linear stability can be lost due to emerging fluctuations or exponential growth [53].

Coexistence: Two or more species are said to coexist if they persist at a positive abundance in the presence of the others. A main force at play against coexistence is *competitive exclusion*, which drives weaker competitive species to extinction [1, 3, 52]. A community state in which all of the initial S species coexist is often called *feasible* [54–56]. Coexistence does not require linear stability: species can persist together although not being at a steady state (e.g. fluctuating abundances), as often observed empirical communities [53, 57].

$$\frac{1}{N_i}\frac{dN_i}{dt} = \frac{r_i}{N_i^{1-k}} - d_i - \sum_{j\neq i}^{S} A_{ij} N_j. \tag{5}$$

As species abundances become small, the per-capita perception of competition (the last term in the right hand side of Eq. 5) decreases linearly. Conversely, the per-capita growth rate (the first term in the right hand side) becomes infinitely large if $k < 1$ (Fig. 1). This leads us to a main ingredient of the SG model: Increasing the number of competitors pushes species towards lower abundances. At low abundance, however, competition becomes smaller while growth becomes extremely large. This has the effect of making the coexistence state more and more stable, so

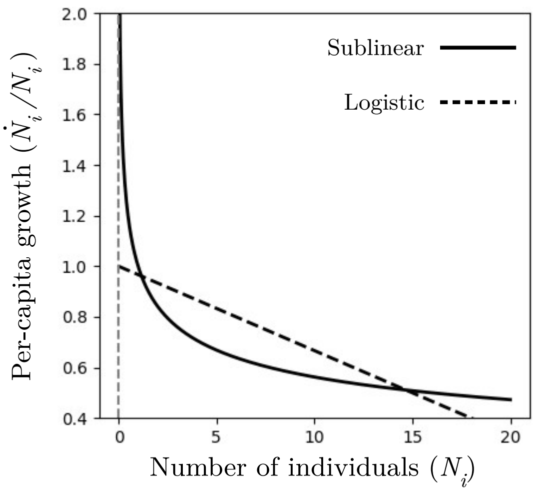

FIG. 1. **Population per-capita growth rates in ecological models**. In the SG model, the population per-capita growth rate $\dot{N}_i/N_i$ (dark line, Eq. 5) diverges at low abundances. Increasing the number of initial species in the SG model drives species to low abundances because of increased competition. Yet, at low abundance, per-capita growth rates becomes extremely large and species can never go extinct due to competition. In the logistic model instead (dashed line), the per-capita growth rate is $r_i(1 - N_i/K_i)$, which is finite at low abundance.

that one could think that initial species diversity favors the coexistence of all species [30] (see Appendix).

If species cannot go extinct in the SG model, competitive exclusion is impossible by definition. As we discuss in detail below, coexistence is then guaranteed by this unrealistic property. Furthermore, the lack of extinctions implies that the model cannot capture other fundamental effects in ecology, such as invasion-extinction processes [58] nor community assembly [59]: any new competitor that is added in a community will decrease the abundance of other species, but will maintain itself and not push any species to extinction. All species that are added in the community will coexist stably.

III. CONSEQUENCES OF DIVERGENT GROWTH ON SPECIES COEXISTENCE

Following the SG model defined by Eq. 4, we study how many species survive (Fig. 2 left) and how many simulations end up in a stable state (Fig. 2 center) when the initial species diversity (S) increases. When all species survive at positive abundances and the final state is stable, the resulting system is said to harbor stable feasibility (Fig.2 right). In the GLV model (Eq. 1), coexistence and stability follow the same trend [12]. Increasing initial diversity first leads to some species going extinct (Fig. 2A), and then leads to the remaining species losing stability (Fig. 2B,

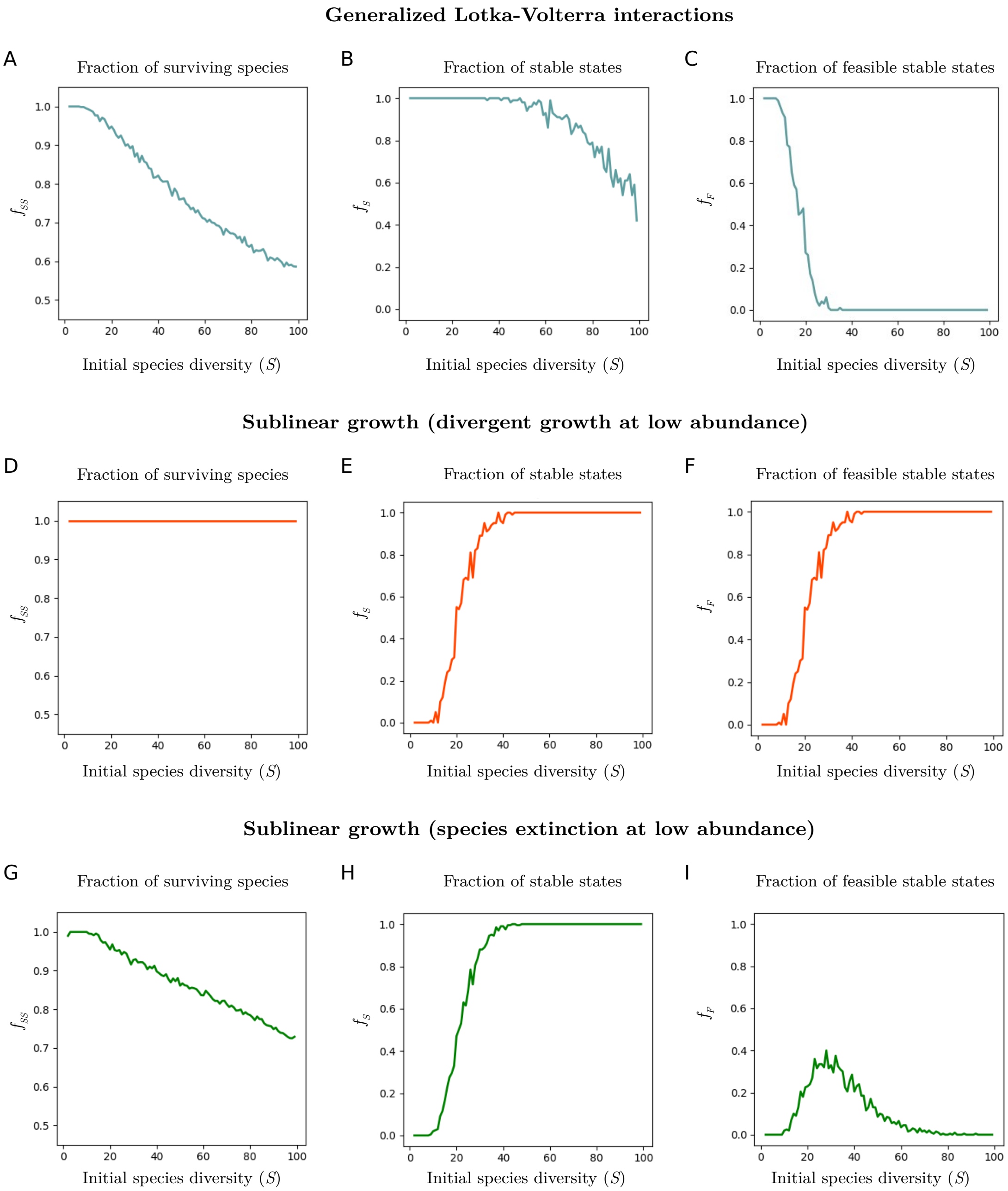

FIG. 2. **Extinctions, stability and stable feasibility under increasing initial diversity**. Here we plot how the initial species diversity (S) modulates the fraction of surviving species at the end of simulations (left), the fraction of stable states (with negative dominant eigenvalue, center) and the probability that a community is both stable and feasible, meaning that all S species coexist (right). We plot the GLV model (A-C) and SG model (D-F) using the parameters of [30], and the SG model with a minimal abundance of $N_m = 2$ below which species go extinct (G-I) (see Appendix). The observation is that diversity increases stability in the SG model, yet diversity has no effect on coexistence, because species can never go extinct [30]. If we allow species to go extinct when their abundance goes below $N_i < N_m = 2$ (G-I), the SG model maintains the trend by which diversity begets linear stability (E,H). Yet, in terms of species coexistence, the model recovers a similar trend as the GLV model: increasing initial diversity leads to competitive exclusion, extinctions and loss of feasibility (G,I).

see Appendix). The combination of both processes implies that increasing species diversity decreases the likelihood of seeing a feasible stable state (Fig. 2C).

In the SG model, instead, increasing initial diversity never drives species to extinctions, as competitive exclusion is artificially impaired by divergent growth. This means that coexistence is not affected by diversity (Fig. 2D), because of the expected *survival of all* effect [23]. Conversely, increasing diversity stabilizes growth and fluctuations. In effect, for systems with a small number of initial species, species grow indefinitely. As diversity increases, competition can control growth dynamics and thus stabilizes the community (Fig. 2E, see Appendix). This new result is the opposite of the negative diversity-stability trend of the GLV model.

The likelihood of finding stable coexistence increases with diversity in the SG model. Yet, this is because initial species diversity increases stability, but has no effect on coexistence (Fig. 2F, Fig. 3A in [30]). This is because in the SG model, all species are always present at positive abundance, independently of the initial diversity or competitive strength of the community. As for the case of models with super-linear death rates [25], unconditional coexistence is likely to be an artificial property of the model.

In sum, the main consequence of divergent per-capita growth rates is that species cannot go extinct. The key underlying mechanism is that increasing species diversity lowers the average species abundances indefinitely, without ever reaching $N_i = 0$. Increasing initial species diversity therefore increases the linear stability of the system (see Appendix and fig. 2E), but species are pushed towards increasingly lower abundances without ever going extinct (Fig. 2D). Below we unpack how diversity modulates species coexistence if species can effectively go extinct when their abundance falls below a certain threshold.

IV. RECONCILING THE MODEL WITH REALISTIC ASSUMPTIONS

We now modify the dynamics to avoid infinite growth at low abundance, while keeping the SG model and the empirical estimates of sublinear scaling in place (Eq. 4, $k = 3/4$). As discussed in [30], one way of doing that is to admit a biomass threshold B_m below which a species go extinct (see Appendix and [30]). In our model, this translates into assuming a minimal number of individuals N_m below which a species becomes extinct. A typical value could be $N_m = 1$ for asexual replicators, or a larger $N_m \geq 2$ for species needing a mate for reproduction (see Appendix and [32]).

In Figure 2 bottom, we plot the same analysis as above but with an extinction threshold for all species at $N_i < N_m = 2$, below which a species is assumed to become extinct (see Appendix). Under this scenario, when diversity increases, species start to go extinct due to competitive exclusion (Fig. 2G). In this more realistic version of the SG model that avoids infinite population per-capita growth rates, species diversity and competition impair species coexistence. The trend by which diversity can stabilize dynamics remains in place (Fig. 2H), providing an interesting mechanism of community self-regulation. Yet, when coexistence of all species and stability are merged to measure stable feasibility, we can see that the SG model rarely finds a stable, species-rich community (Fig. 2I): either dynamics are unstable at low diversity, or species go extinct at high diversity. As expected, the fraction of extinct species depends on the location of the extinction threshold. Assuming more or less strict thresholds, either in terms of minimal biomass or abundance of individuals, implies a stronger or weaker impact of competitive exclusion (see Appendix).

The same result emerges from applying other mechanisms that limit the diverging growth rate in the SG model. This can be done without imposing species extinctions, e.g. by assuming that population growth rates are linear or constant instead of divergent below a certain threshold (see S5.2 of [30]).

As discussed when introducing the model, the *survival of all* effect in the SG model also depends on a deeper assumption: growth rates scale sublinearly with abundance (N_i^k), while death and the perceived impacts of competition are linear ($-d_i N_i$) and bilinear ($-N_i A_{ij} N_j$). Previous research showed that *survival of all* effects can also happen when growth rates are linear (N_i), but death rates are super-linear ($-d_i N_i^{1+k}$) [25, 60]. Consistently, as recently shown in [41], unconditional coexistence without species extinctions emerges whenever the scaling of growth rate with species abundance is smaller than the perception of death and competition. Following [30, 41], one could assume a variation of the original SG model where all exponents are different from 1,

$$\frac{dN_i}{dt} = r_i N_i^k - d_i N_i^{a+b} - N_i^a \sum_{j \neq i}^{S} A_{ij} N_j^b. \tag{6}$$

Now a and b capture how intra- and interspecific interactions impact the growth of x_i. This variation of the SG model recovers the SG model above if $k = 3/4$ and $a = b = 1$, and the GLV model if $k = a = b = 1$. However, one could also assume that both population growth (k) and interspecies interactions scale sublinearly with species abundance ($k, a, b < 1$). In this scenario, as soon as $k = a$, one recovers a similar behavior as in the GLV model: increasing diversity impairs species coexistence (Fig. 2 top, see [41] for a thorough discussion). This is because, in such systems, having more species coexist amounts to solving a linear problem with increasingly more constraints, which rapidly becomes impossible.

It remains unclear whether we can assume that the scaling exponents of growth and interactions are different ($k \neq a$). For example, [39] provides a recent empirical observation of tree-tree interactions also scaling sublinearly with biomass, while [33, 37, 38, 40, 42, 61] discuss different scenarios of sublinear predator-prey and consumer-resource interactions.

Cellular replication in solid tumors provides another interesting example of growth and competition exponents being possibly equivalent: one can consider that growth happens at the surface of the tumor where nutrients are available [62]. Resource competition with other cells or the attack of immune cells, which hardly penetrate the tumor, is also a surface process [63]. In that case, both growth (k) and interactions (a, b) would be sublinear with total tumor biomass, as only the populations at the surface interact, and coexistence would not be guaranteed [41].

To conclude, increasing the realism of the SG model, e.g. by introducing a minimal abundance threshold below which a species goes extinct or assuming equivalent density dependent exponents, results in the same paradox as in previous models: increasing the number of competing species decreases the likelihood of their coexistence.

V. LOOKING AHEAD

In the present work, we have discussed how diversity modulates stability and species coexistence in the SG model. Our intention has been to unpack in simple terms recent results on the SG model [30] and relate them to earlier work of prebiotic replicators [20, 23] and non-linear density-dependent effects [25].

On the one hand, diversity and competition can stabilize population growth in the SG model, uncovering a novel potential mechanism of community-level regulation of fluctuations [30, 41]. This is a new and important result for theoretical community ecology: it opens the door towards a more nuanced understanding of how population growth, interspecies interactions and community stability might be intertwined in natural ecosystems.

On the other hand, however, the absence of species extinctions in the SG model implies that competitive exclusion is impossible by definition. Hence, coexistence in the SG model emerges artificially and the model might fail at describing key ecological processes such as extinction-invasion dynamics and community assembly. The SG model can be reconciled with species extinctions by assuming non-infinite population growth at low species abundance. Yet, when this is done, we recover the expected trend previously found in the GLV model: increasing species diversity leads to species extinctions and competitive exclusion.

The behaviors of SG models under mutualistic, predatory and consumer-resource interactions remain open research questions [33, 42, 61]. For the case of mutualism, as it happens in the GLV model, species are likely to undergo exponential growth in the SG model unless the benefits of mutualism follow a saturating function (see e.g. [64]). For predator-prey interactions, recent results have studied whether SG of prey [65] or else sublinear inter-specific predation rates [61] could explain observations of predator-to-prey biomass scalings. In models of consumer-resource interactions, recent results propose that sublinear consumption rates could provide a bypass from *one resource-one* *consumer* limitations, so that multiple species could stably survive on a single resource [30]. Future studies should accurately analyze how these results are affected by the divergent behavior and absence of species extinctions in SG models.

Because species and ecosystems are increasingly endangered and their habitats and populations are under threat, a fundamental task of ecological models is to help us understand and predict the conditions by which species can coexist without going extinct. Is coexistence a matter of satisfying abiotic and biotic constraints, so that the more species, the more constraints there are to satisfy? If so, high diversity of natural ecosystems would imply, as Robert May put it, the existence of 'devious strategies' in nature that allow species to stably coexist. But it could also be that biodiversity itself favours species coexistence, as it is clear that some species allow others to persist, directly or indirectly. The SG model suggests that the former 'coexistence as constraints' perspective might only emerge from the mathematical specificity of assuming linearity in both population growth and interspecies competition. By relaxing the assumption of linearity of population growth curves, the SG model proposes that competition amongst species is no longer a constraint for coexistence. This, however, might not be so simple; we have clarified here how the surprising behaviour of the SG model comes from an artificial singularity at low species abundance, whereas the effects of sublinear growth at high species abundance remain to be studied. Overall, understanding the impacts of non-linear density dependent effects on species coexistence, as well as their relation with the many coexistence mechanisms proposed in the literature, will contribute to our fundamental understanding of community ecology.

Appendix

Rescaling from biomass to individuals: One recently proposed version of the SG model is written in terms of species biomass, B_i, instead of the number of individuals [30]. By using macro-ecological biomass data, the authors in [30] propose an estimate of $k = 3/4$ and the subsequent SG model

$$\frac{dB_i}{dt} = r_i B_i^k B_0^{1-k} - d_i B_i - B_i \sum_{j \neq i}^{S} A_{ij} B_j,$$

It is interesting to rescale the model from biomass B_i to the number of individuals N_i, as presented in our work. To do so, one can assume a typical biomass of an individual of species i to be $B_{0,i}$, which can be equivalent to the typical biomass at which growth is r_i (see below). Then, the number of individuals is $N_i = B_i / B_{0,i}$, and to rescale the equation we divide in both sides by $B_{0,i}$

$$\frac{dN_i}{dt} = r_i B_0^{1-k} B_{0,i}^{k-1} \left(\frac{B_i}{B_0} \right)^k - d_i \frac{B_i}{B_{0,i}} - \frac{B_i}{B_{0,i}} \sum_{j \neq i}^{S} A_{ij} B_{0,j} \frac{B_j}{B_{0,j}},$$

and one reaches Eq. (4) by rescaling competitive strengths by typical abundances $\widetilde{A}_{ij} = A_{ij} B_{0,j}$ and assuming all species have the same typical biomass $B_{0,i} = B_0 \; \forall i$. The tildes to discern between abundance and biomass interaction matrices are later discarded throughout the main text.

Typical biomass B_0 and minimal abundance for replication N_m: The term B_0 in the equation above locates the typical biomass at which growth per unit of biomass equals the characteristic growth rate. If $B_i = B_0$, $G(B_i = B_0) = r_i B_i^k B_0^{1-k} = r_i B_0$, and in terms of growth per unit of biomass, one can write $G(B_i = B_0)/B_i = r_i$. If we define B_0 to be the typical biomass of an individual, this term is then the per-capita growth rate of species i (Eq. 5). This can be used to define a minimal biomass threshold: if the highest growth rate observed in a species is r_i, then one would need that growth below a given B_m is no longer sublinear (see e.g. supplementary materials of [30], section S5.2). By imposing non-divergent growth or even extinction below B_m, one recovers the condition by which excessive diversity disrupts species coexistence. Interestingly, if B_0 is the typical biomass of an individual of a given species, imposing a minimal biomass for growth is equivalent to assuming that a species cannot growth if N_i, the number of individuals, is below a certain threshold. For non-sexual replicators, the extinction threshold of $N_m = 1$ is equivalent to imposing a threshold biomass at $B_m = B_0$, equal to the characteristic biomass of an individual. For sexual replicators, the minimal abundance to overcome extinction is likely to be considerably higher [32].

The effect of varying the extinction threshold N_m: As shown in [30] and discussed in main text, imposing a minimal abundance below which a species goes extinct corrects the effects emerging from diverging population per-capita growth rate at low abundance. This specific mechanism equates to imposing a strong Allee effect on all species [32]. As expected, the likelihood that species coexist or else start to go extinct depends on the location of the threshold. As seen in figure 3, increasing the minimal abundance from $N_m = 2$ to $N_m = 4$ or decreasing it to $N_m = 1$ reduces the likelihood of stable feasibility as species become extinct earlier. This corresponds to increasing the minimal biomass threshold from $B_m = 2B_0 = 0.03$ to $B_m = 4B_0 = 0.06$ or decreasing it to $B_m = B_0 = 0.015$ in the biomass parametrization of [30] (see below).

Parameter choices: The figures are based on replicating the studies in [30]. Because dynamics in [30] are expressed in terms of biomass, the rescaling proposed above can be done by assuming that one individual has typical biomass of $B_0 = 0.015$, and hence the threshold of two individuals for survival is equivalent to $B_m = 2B_0 = 0.03$. This is necessary to translate the parametrization of [30] into a species abundance model based on N_i. In figure 1, we use $r = 1$, $d = 0$ for the sublinear per-capita growth rate function and $r = 1$ and $K = 20$ for the logistic per-capita growth rate function, without species interactions (single-species population growth, $A_{ij} = 0 \; \forall \; i \neq j$). The parameters are taken only for illustrative purposes so that the two growth functions are comparable. In figure 2 we replicate the parameters used in Figure 3A of [30]: $r = 1$, $d = 0$, $k = 3/4$, and take $K = 1$. The parameters of the interaction matrix are sampled from a normal distribution with $\mu = 0.2$ and

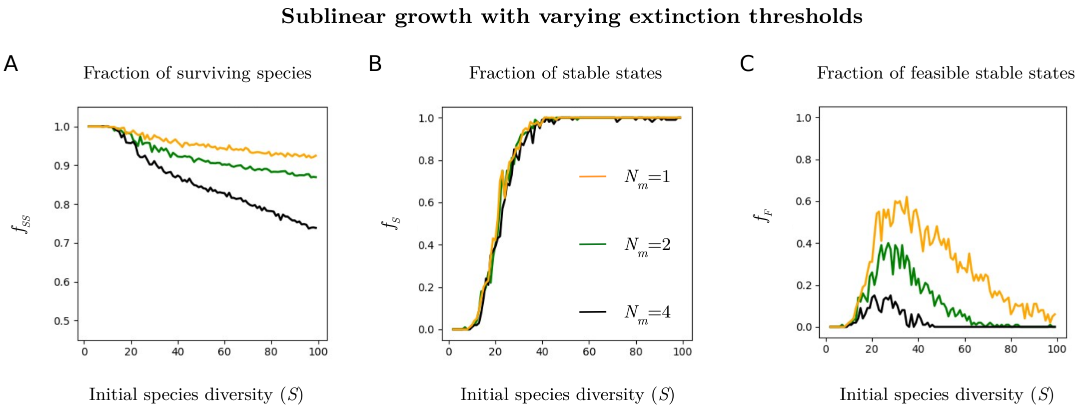

FIG. 3. **(Appendix Figure) Increasing the extinction threshold reduces the likelihood of coexistence**.Here we replicate figure 2.I regarding how diversity modulates the fraction of surviving species (A), the fraction of linearly stable states (B) and the fraction feasible stable states (C). We now impose three different thresholds of species extinction, at $N_m = 1$ (orange), $N_m = 2$ (green) and $N_m = 4$ (black). As expected, increasing the threshold decreases the likelihood of species coexistence, as species go extinct at higher abundance.

$\sigma = 0.1$, equivalent to $\mu = 0.01$ and $\sigma = 0.005$ in [30] once renormalized by carrying capacity, and ensure that all interaction terms are positive to avoid cooperative interactions. The expected diversity threshold of the GLV model is $S \approx 128$, computed from $\sigma^c = \sqrt{2/S}(1+\mu)$ [10, 11, 35]. In figure 2 bottom we add a minimal abundance of $N_m = 2$, below which the abundance of a species is set to zero. This is equivalent to setting $B_m = 2B_0 = 0.03$ in [30], so that we are assuming that a single individual has a biomass of $B_0 = 0.015$. Equivalent qualitative results as those of figure 2 are obtained when species do not directly become extinct below threshold, but only reduce their growth rate to avoid infinitely large values (not shown, but see supplementary section S5.2 of [30]).

Simulating the dynamics: Simulations in figure 2 are implemented by solving model (4) with a Runge-Kutta method of order 5(4) [66] via the solve_ivp function of the scipy.integrate_library, and we replicate the numerical methods described in [35, 67] to assess stability and surviving species. For each integer species value (x-axis), we generate 100 different interaction matrices A. For each, we generate random positive initial conditions with $N_i(t=0) \in [0, 33]$ and run the dynamics for 1000 timesteps. After those, we compute the average number of species with strictly positive abundance over the 100 simulations (panel A), the fraction of simulations where all species abundances remain equivalent after 100 additional timesteps and the dominant eigenvalue of this state is negative (panel B) and the fraction of simulations in which the final state is stable and all species coexist at strictly positive abundance (panel C). The codes to generate figure 2 as well as additional codes to explore properties of the SG model are available at: https://anonymous.4open.science/r/Unpacking-Sublinear-Growth-0918

Linear stability and species extinctions: The particular behavior of the SG model at low abundance and its impact on stability and the lack of species extinctions can be understood by studying the Jacobian of the system. In the absence of an extinction threshold, the fixed state of the system fulfills

$$\frac{dN_i}{dt} = r_i N_i^k - d_i N_i - N_i \sum_{j \neq i}^{S} A_{ij} N_j = 0,$$

so that, because N_i will never get to zero, the fixed state abundances N_i^* can be found by dividing by N_i and solving the following expression

$$r_i (N_i^*)^{k-1} - d_i - \sum_{j \neq i}^{S} A_{ij} N_j^* = 0.$$

What is the stability of this state? The diagonal elements of the Jacobian matrix evaluated at N^* follow

$$\mathcal{J}_{ii} = \frac{\partial}{\partial N_i} \frac{dN_i}{dt} = k r_i N_i^{k-1} - d_i - \sum_{j \neq i}^{S} A_{ij} N_j |_{N=N^*}$$

and applying the expression for the stable state,

$$\mathcal{J}_{ii} = -\frac{(1-k) r_i}{(N_i^*)^{1-k}}.$$

The off-diagonal elements of the Jacobian are

$$\mathcal{J}_{ij} = \frac{\partial}{\partial N_j} \frac{dN_i}{dt} = -N_i^* A_{ij}.$$

The complete Jacobian matrix writes

$$\mathcal{J} = \begin{pmatrix} -\frac{(1-k)r_1}{(N_1^*)^{1-k}} & \cdots & -N_1^* A_{1S} \\ \vdots & \ddots & \vdots \\ -N_S^* A_{S1} & \cdots & -\frac{(1-k)r_S}{(N_S^*)^{1-k}} \end{pmatrix}.$$

Increasing the number of species decreases their biomass due to competition. In that context, the off-diagonal terms emerging from interspecies competition become small. Yet, the diagonal terms, representing self-regulation, become divergingly negative towards minus infinity, pushing the eigenvalues towards more and more negative values. This is how stronger competition can lead to a more stable state: increasing S makes the coexistence state divergingly stable.

Conversely, one can study the stability of the state with some species extinct ($N_i = 0$). In this state, the diagonal terms of the new Jacobian diverge towards positive infinity, making competitive exclusion unstable for any parameter setting (and, in fact, impossible to attain by the dynamics). This is equivalent to showing that any absent species can always invade in the community: because invasion growth rates – the diagonal elements of the new Jacobian – diverge at low abundance, rare invaders will always be able to invade while at the same time not driving other species to extinction.

Acknowledgements

The authors thank O. Mazzarisi and the other authors of [30] for positive and constructive discussions. G.A-G. thanks C. Jacquet for insightful revision and feedback on the manuscript, R. Solé and T. Gross for pointing towards earlier results and bibliography and M. Barbier, Ll. Arola-Fernandez, B. Pichon, M. Lutterman and N. Humbert for insightful discussions. Special thanks to T. Claramunt for inspiration. G.A-G. was supported by a 2022 postdoctoral fellowship of the Fundación Ramón Areces and a Marie Skłodowska-Curie Actions Postdoctoral Fellowship under project FRAGILEPRINTS - 101105029. Views and opinions expressed are however those of the author(s) only and do not necessarily reflect those of the European Union or the CNRS. Neither the European Union nor the CNRS can be held responsible for them. J-F.A. was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41).

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