Will a small randomly assembled community be feasible and stable?

Chuliang Song and Serguei Saavedra[2]

Department of Civil and Environmental Engineering, MIT, 77 Massachusetts Avenue, Cambridge, Massachusetts 02139 USA

Abstract. How likely is it that few species can randomly assemble into a feasible and stable community? Some studies have answered that as long as the community is feasible, it will nearly always be stable. In contrast, other studies have answered that the likelihood is almost null. Here, we show that the origin of this debate has been the underestimation of the association of the parameter space of intrinsic growth rates with the feasibility and stability properties of small randomly-assembled communities. In particular, we demonstrate that not all parameterizations and sampling distributions of intrinsic growth rates lead to the same probabilities of stability and feasibility, which could mistakenly lead to under- or overestimate the stability properties of feasible communities. Additionally, we find that stability imposes a filtering of species abundances "towards" more even distributions in small feasible randomly-assembled communities. This indicates that the stability of feasible communities is inherently linked to the starting distribution of species abundances, a characteristic that many times has been ignored, but should be incorporated in manageable lab and field experiments. Overall, the return to this debate is a central reminder that a more systematic exploration of the feasible parameter space is necessary to derive general conclusions about the stability properties of ecological communities.

Key words: feasibility; intrinsic growth rates; random matrices; small communities; species abundances; stability.

Introduction

Traditionally in ecology, the term *feasibility* has been used to denote the property of a community of having all of its constituent species with positive abundances at equilibrium (Roberts 1974). Feasibility then becomes a necessary condition for species persistence (Hofbauer and Sigmund 1998). However, because community dynamics cannot be understood without attention to environmental perturbations (Levins 1968, Saavedra et al. 2013), feasibility does not always guarantee species persistence (Hofbauer and Sigmund 1998). Thus, the term *stability* has been widely used to denote the small or large friction forces acting against perturbations (Lewontin 1969). In fact, it has been shown that under specific dynamics, the global stability of a feasible community does imply species persistence (Hofbauer and Sigmund 1998). Because communities are seldom at equilibrium due to the constant perturbations coming in abundance from the environment, from the perspective of a randomly-assembled community, both feasibility and stability conditions become important descriptors of the dynamical space in which the community is evolving (Lewontin 1969).

In this context, theoretical work in ecology has demonstrated that it is highly improbable that a large number of species can spontaneously and randomly assemble into a feasible and stable community (May 1972). This theoretical work has been derived for communities whose size tends to infinity, and it has shown that stable communities will only emerge as long as a derived measure of community complexity is below a certain threshold (May 1972). This complexity measure has been defined as $\sigma\sqrt{S \times C}$, where σ represents the standard deviation of the distribution of interaction strengths, S corresponds to the number of species in the community, and C corresponds to the connectance in the community (i.e., number of direct interspecific interactions out of the possible direct interactions in the community). As long as $\sigma\sqrt{S \times C} < 1$, it has been shown that large randomly-assembled communities can be stable, regardless of other parameters in the system (May 1972). While our understanding about the stability properties of large randomly-assembled communities is substantial (Allesina and Tang 2015), the relatively simpler question of whether a small randomly-assembled community will emerge into a feasible and stable community has no unified answer (Pimm 1982). Yet, it is biologically more likely to see small rather than large communities assembling at random, especially during initial successional stages (Odum 1969, Saavedra et al. 2017a).

To investigate small randomly-assembled communities, studies in the 1970's combined general population dynamics models and random matrix theory (Roberts 1974, Gilpin 1975, Goh and Jennings 1977). In particular, they considered the time evolution of populations following the classic Lotka-Volterra (LV) system of the form

$$\frac{dN_i}{dt} = N_i \left(r_i + \sum_{j=1}^{S} a_{ij} N_j \right) \qquad (1)$$

where N_i corresponds to the abundance (or biomass) of species i, $\mathbf{A}$ is the interaction matrix whose elements a_{ij} correspond to the direct effect of species j on species i, r_i is the intrinsic growth rate of species i, and S corresponds to the number of species in the community (Case 2000). Note that the value of intrinsic growth rates are inherently linked to environmental conditions (Levins 1968, Roughgarden 1975, Cadotte and Tucker 2017).

The parameterization of the random interaction matrix $\mathbf{A}$ was done in the following way. The diagonal elements were taken as $a_{ii} = -1 \; \forall \; i$ (Roberts 1974), introducing the biological principle of self-regulation (Case 2000). Other studies (Gilpin 1975, Goh and Jennings 1977) also considered taking values of $a_{ii} = 1$ with a more mathematical rather than a biological motivation. In fact, the lower the fraction of negative diagonal values is, the larger the eigenvalues representing the rate of divergence of perturbations (McCann 2011), and in turn, the lower the likelihood of stable communities (see Appendix S1). Then, each off-diagonal element a_{ij} ($i \neq j$) was set to take with probability C a random value drawn from a normal probability distribution (with mean zero and variance σ^2), $a_{ij} = 0$ otherwise. Note that $0 < C \le 1$ corresponds to the connectance of the community, and σ corresponds to the standard deviation of the distribution of interaction strengths, illustrating the interpretation of the complexity measure mentioned before for randomly-assembled communities. This parameterization then generates sensible distributions of interaction matrices (Murdoch et al. 2003, Olff et al. 2009). That is, a random ensemble of self-regulating species, where on average one-half of the ensemble is characterized by predator–prey dynamics, one-quarter by mutualistic dynamics, and the other one-quarter by competition dynamics.

Note that the biological assumptions of the LV model correspond to the case where the ith species dynamics in the absence of all the others is given by the logistic equation (i.e., self-limitation), and the effect on the jth species on the ith species is proportional to the product of their biomasses, following the hypothesis of encounters and equivalences (Logofet 1993, McCann 2011). It is also assumed that the natality of producers is limited physiologically. In general, it is assumed that mortality functions are constant and preying functions are linear (which holds for low concentrations of food) under closed systems.

The stability of the community was investigated through the lens of local asymptotic stability (May 1972). That is, the friction forces acting at the equilibrium point against small perturbations to species abundances. The biological implications of this type of stability have been debated (Ives and Carpenter 2007), but stronger conditions of stability have been difficult to derive for random matrices (Logofet 1993). Nevertheless, local stability still provides information about the neighborhood friction forces acting on communities (Lewontin 1969). Local stability is fulfilled when all the eigenvalues of the Jacobian matrix ($\mathbf{J}$) when evaluated at the equilibrium point ($\mathbf{N}^*$, as defined by $d\mathbf{N}^*/dt = 0$) have negative real parts (Case 2000). For LV dynamics, the Jacobian is defined as

$$\mathbf{J} = \text{diag}(\mathbf{N}^*) \cdot \mathbf{A} \qquad (2)$$

where $\mathbf{N}^*$ corresponds to the vector of species abundances at equilibrium and $\text{diag}(\cdot)$ represents a diagonal matrix. The debate was centered on whether randomly-assembled communities with a feasible equilibrium ($\mathbf{N}^* > 0$) will always be stable (Roberts 1974, Gilpin 1975, Goh and Jennings 1977). To test this idea, studies calculated the probability of local stability of small randomly-assembled communities by generating random matrices $\mathbf{A}$ as defined above, arbitrarily parameterizing the vector $\mathbf{r}$ of intrinsic growth rates, and looking at the fraction of feasible communities satisfying local stability. Feasible equilibrium points can be extracted by solving the interior equilibrium given by $\mathbf{N}^* = -\mathbf{A}^{-1}\mathbf{r}$ (see Appendix S1 for more details about the calculation of this equilibrium).

In particular, the first set of studies (Roberts 1974) fixed the intrinsic growth rates to $r_i = 1 \; \forall \; i$, meaning, for instance, that all species could have the exact same metabolic rate. Note that for a species i in isolation, a value of $r_i = 1$ and $a_{ii} = -1$ correspond to a nondimensionalized logistic growth equation (Case 2000). These studies found that the probability of local stability for the feasible communities was almost 100% (see red circles in Fig. 1a), concluding that small feasible communities are nearly always stable (Roberts 1974). This result can be attributed to the fact that this type of parameterization generates feasible communities that are diagonally stable, a sufficient condition for stability (although these patterns are not robust for all types of parameterization, see Appendix S1; Logofet 1993, Stone 2016).

In contrast, subsequent studies (Gilpin 1975, Goh and Jennings 1977) allowed intrinsic growth rates to change randomly and uniformly between $-1 < r_i < 1$ (originally, the parameterization was set to $r_i = 1$ or $r_i = -1$ yielding the same results). This parameterization implies no structure nor dependency whatsoever between intrinsic growth rates. By extracting the feasible communities from this parameterization, this work showed that the probability of local stability for these small feasible communities was nearly null (see gray squares in Fig. 1a). These studies also showed that the fraction of randomly-assembled feasible communities generated with a random parameterization of intrinsic growth rates decreases as a function of the number of species in the community as 2^{-S} (Gilpin 1975, Goh and Jennings 1977). In fact, randomly-assembled feasible communities were more difficult to be found with the random parameterization than using the fixed vector $r_i = 1 \; \forall \; i$ (see Fig. 1b). This suggested that the probability of observing a small, feasible, stable, randomly-assembled community is almost negligible.
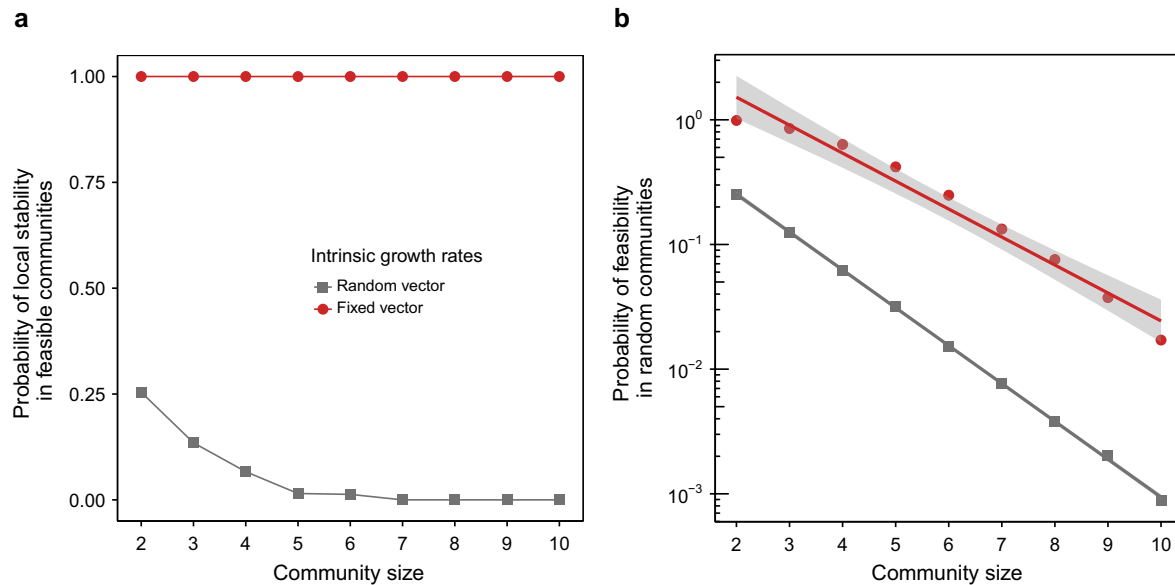
a

b

FIG. 1. Contrasting answers to a relatively simple question. Following a classic Lotka-Volterra system, panel a shows that fixing the intrinsic growth rates to $r_i = 1 \; \forall \; i$ (Roberts 1974), the probability that a small, feasible, randomly-assembled community is locally stable is basically 100% (red circles). In contrast, sampling randomly and uniformly values between $-1 < r_i < 1$ (Gilpin 1975, Goh and Jennings 1977), the probability is basically null (gray squares). In panel b, we show the fraction (on a log scale) of feasible communities obtained from the randomly assembled communities with the parameterizations used in panel a. The regression lines are depicted with shaded 95% confidence intervals. Only for replicability purposes of the debate (Gilpin 1975, Goh and Jennings 1977), these two plots use the same parameters as the original work: a normal distribution for the construction of the interaction matrix, $C = 1$, $\sigma = 0.4$, and 70% of the diagonal elements are $a_{ii} = -1$, the rest are set to $a_{ii} = 1$ (regardless of community size). Probabilities are calculated from 10,000 simulations. Quantitative results can change due to parameterization (see Appendix S1).

However, all of this work relied on either random or arbitrary parameterizations of intrinsic growth rates, and little is known about whether these results hold under a more systematic analysis of the parameter space of intrinsic growth rates. In fact, theoretical work today continues to overlook the role of the structure of intrinsic growth rates in shaping the feasibility and stability of ecological communities (James et al. 2012, Coyte et al. 2015, Wootton and Stouffer 2016), generating little intuition about how this debate should be resolved. Here, capitalizing on recent advancements characterizing the feasible parameter space (also known as feasibility domain) of ecological communities (Rohr et al. 2014, Saavedra et al. 2017b), we go back to study systematically this important debate in ecology.

METHODS

Instead of trying naively (and very likely unsuccessfully) to obtain a representative sample of the combinations of intrinsic growth rates leading to feasible communities by random sampling, we can systematically investigate the feasibility domain of these communities. The feasibility domain of a community defined by LV dynamics over a given interaction matrix **A** corresponds to all the vectors of intrinsic growth rates leading to positive equilibria (Logofet 1993, Rohr et al. 2014). It can

be proved (Logofet 1993, Saavedra et al. 2016b, 2017b) that this feasibility domain $D_F(\mathbf{A})$ is an algebraic cone described by

$$D_F(\mathbf{A}) = \left\{ \mathbf{r} = N_1^* \mathbf{v}_1 + \cdots + N_S^* \mathbf{v}_S, \text{with } N_1^* > 0, \cdots, N_S^* > 0 \right\} \tag{3}$$

where N^* is the equilibrium abundance of species i, and $\mathbf{v}_i$ is the spanning vector (also called an extreme ray in convex geometry; Bertsimas and Tsitsiklis 1997) of the algebraic cone, whose jth component is the normalized column vector jth of the interaction matrix **A**

$$\frac{-A_{ji}}{\sqrt{\sum_{k=1}^{S} A_{ki}^2}}. \tag{4}$$

This means that a community will always be feasible with any direction of vectors of intrinsic growth rates falling inside the bounded feasibility domain $\mathbf{r_f} \in D_F(\mathbf{A})$ defined by

$$\mathbf{r_f} = \sum_{k=1}^{S} N_k^* \mathbf{v}_i \tag{5}$$

where N_k^* are all values in $(0, 1)$, and $\sum_{k=1}^{S} N_k^* = 1$. It can be proved that the norm does not affect the qualitative

results (Rohr et al. 2016). In other words, whether we normalize the spanning vectors or not, the direction of the vectors $\mathbf{r_f}$ of intrinsic growth rates leading to feasible species abundances is the same. Only by changing the elements of the interaction matrix $\mathbf{A}$, it is possible to change the direction of the vectors that fall inside the feasibility domain $D_F(\mathbf{A})$. Importantly, this also implies that there is a one-to-one mapping between the intrinsic growth rate space and the species abundance space at equilibrium (Logofet 1993, Rohr et al. 2016).

Because this feasibility domain is a bounded region, it also has a geometric centroid specified by the vector of intrinsic growth rates

$$\mathbf{r_c} = \frac{1}{S}\mathbf{v}_1 + \cdots + \frac{1}{S}\mathbf{v}_S. \tag{6}$$

This direction of vectors has an important ecological meaning. It is the vector that can tolerate, on average, the largest random perturbation to intrinsic growth rates without pushing species "toward" extinction (Rohr et al. 2014, 2016, Saavedra et al. 2014, 2017b). Note that extinctions would occur if the new perturbed vector falls outside of the feasibility domain. Importantly, this vector $\mathbf{r_c}$ is by construction dependent on all the species present in the community, and should not be taken as an image of a random-assembly process (Saavedra et al. 2017b).

Alternatively, for any given interaction matrix $\mathbf{A}$, one can always set a given feasible equilibrium point ($\mathbf{N}^* > 0$) and then calculate the corresponding vector of intrinsic growth rates ($\mathbf{r}^* = -\mathbf{A}\mathbf{N}^*$). In contrast, as shown in Fig. 1, if we use a random or a fixed vector of intrinsic growth rates, it will unlikely lead to a feasible community (e.g., for $r_i = 1 \ \forall \ i$ then $\mathbf{N}^* = -\mathbf{A}^{-1} \cdot \mathbb{1}$). See Fig. 2 for a graphical example of the location of all these vectors of intrinsic growth rates relative to the feasibility domain.

Similarly, if one is interested in a perfect even distribution of abundances (i.e., $N_i^*=1 \ \forall \ i$), then the feasible vector is simply $\mathbf{r}^* = -\mathbf{A} \cdot \mathbb{1}$, where $\mathbb{1}$ represents the identity matrix. In fact, for randomly-assembled communities with a symmetric construction, it has been shown that the closer the vector of intrinsic growth rates gets to the geometric centroid of the feasibility domain, the more even the distribution of abundances among species (Rohr et al. 2016). Thus, for the specific case of the vector $\mathbf{r_c}$ defining the centroid of the feasibility domain, the Jacobian matrix $\mathbf{J}$ is proportional to the interaction matrix as defined in Eq. 2. Note that under May (1972)'s approach the stability of the community is dependent only on the properties of the community matrix. Under LV dynamics, this implies that the vector $\mathbf{r_c}$ defining the centroid of the feasibility domain needs to be used to recover May (1972)'s approach.

Then to systematically study the feasibility-stability debate in small randomly-assembled communities, we generated random matrices $\mathbf{A}$ as defined in the introduction, fixed the level of complexity ($\sigma\sqrt{S \times C}$) across different community size, sampled methodologically 10,000
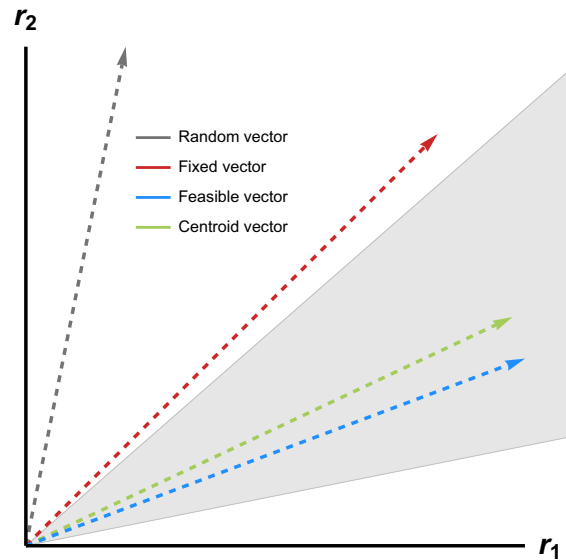

FIG. 2. Graphical example of vectors of intrinsic growth rates relative to the feasibility domain. For a hypothetical interaction matrix $\mathbf{A}$ with two species, the figure shows the parameter space defined by the two intrinsic growth rates of the species (r_1 and r_2). Inside this parameter space, the figure shows the feasibility domain $D_F(\mathbf{A})$ (gray region), the geometric centroid of $D_F(\mathbf{A})$ (green vector), a feasible vector $\mathbf{r_f}$ sampled randomly inside $D_F(\mathbf{A})$ (blue vector), the fixed vector $\mathbf{r} = [1, 1]$ (red vector), and a vector sampled completely randomly (gray vector). Note that each vector corresponds to a combination of the two intrinsic growth rates, and $D_F(\mathbf{A})$ corresponds to all the vectors leading to a feasible community (i.e., $\mathbf{N}^* = -\mathbf{A}^{-1}\mathbf{r} > 0$). Note that there is a one-to-one mapping between the intrinsic growth rate space and the species abundance space at equilibrium (Rohr et al. 2016).

feasible and random vectors of intrinsic growth rates, and calculated the probability of local stability of these small randomly-assembled communities. While the measure of community complexity was derived for communities whose size tends to infinity (May 1972), it provides a good benchmark and approach to compare communities with different size (as shown in Fig. 1a, the probability of stability is also dependent on the level of complexity). For illustration purposes, we defined three levels of complexity: low, medium, and high complexity with values of 0.1, 0.5, and 2.0, respectively. Recall that the stability threshold is $\sigma\sqrt{S \times C} < 1$. All random interaction matrices are generated following a normal distribution, diagonal elements are set to $a_{ii} = -1 \ \forall \ i$, and connectance is set to $C = 0.4$. Results are qualitatively the same with different parameterizations (see Appendix S1). Thus, the level of complexity was adjusted for each community size S simply by changing the value of the standard deviation of interaction strength σ. Recall that this process can change the feasibility domain of communities.

To methodologically sample vectors of intrinsic growth rates, we used four different parameterizations. The first parameterization has the values randomly and uniformly

chosen between $-1 < r_i < 1 \ \forall \ i$, as defined by Goh and Jennings (1977). The second parameterization has the values of intrinsic growth rates fixed to $r_i = 1 \ \forall \ i$, as defined by Roberts (1974). The third parameterization has the values sampled randomly inside the feasibility domain ($\mathbf{r_f}$), as defined above. The fourth parameterization has all the values defined by the geometric centroid of the feasibility domain ($\mathbf{r_c}$), as defined above. Note that the first and second parameterizations are chosen for illustrative purposes of the debate. Our parameterization of intrinsic growth rates takes into account all possible values $\in \mathcal{R}^S$. This means that results derived from this parameterization correspond to the largest sample space possible for the random assembly of a community. To introduce constraints to intrinsic growth rates, one would need to invoke energy conservation principles or physiological

limits, which fall outside of the scope of this work. Yet, we believe future work should investigate the effect of these potential constraints.

RESULTS

First, we confirmed that there is always a bounded region of intrinsic growth rates under which a small randomly-assembled community can be feasible. Fig. 3 panels a–c shows the probability of feasibility for all randomly-assembled communities across the gradients of community size and community complexity. As expected, using both the feasible vectors $\mathbf{r_f}$ (blue triangles) and centroid vectors $\mathbf{r_c}$ (green stars), all communities are always feasible regardless of the level of complexity and community size. In contrast, the fixed vectors (red circles) yield
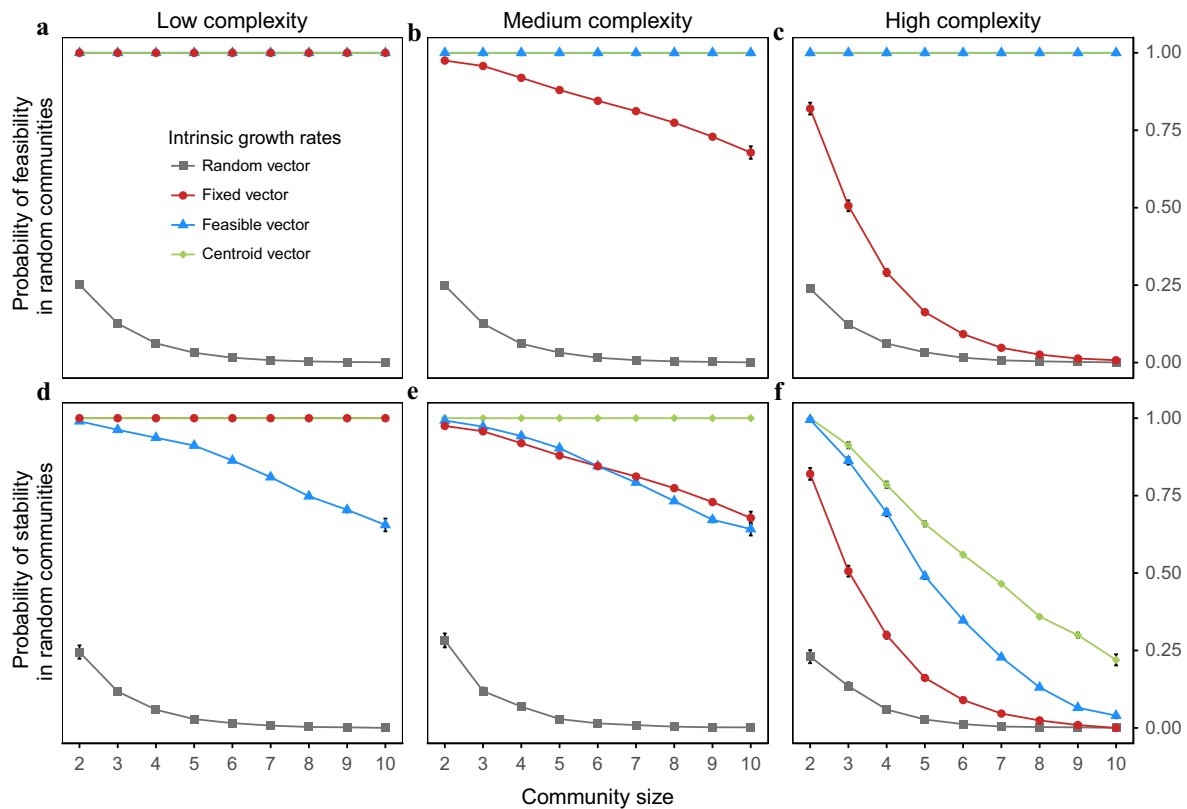

FIG. 3. The stabilizing effect of feasible randomly assembled communities. For different parameterizations of intrinsic growth rates, Panels a–c show the probability of feasibility in randomly-assembled communities (similar to Fig. 1b) as a function of both the level of community size and complexity. Panels d–f show the probability of stability in randomly-assembled communities. Per May (1972), community complexity is defined as $\sigma\sqrt{S \times C}$, where σ is the standard deviation of the distribution of interaction strengths, C is connectance, and S is community size. Here low, medium, and high complexity are defined with values of 0.1, 0.5, and 2.0, respectively. All random interaction matrices are generated following a normal distribution, all diagonal elements are set to $a_{ii} = -1$, and $C = 0.4$. The level of complexity was adjusted for each community size S simply by changing the value of σ. For the parameterization of vectors of intrinsic growth rates, gray squares correspond to vectors chosen randomly between $-1 < \mathbf{r_i} < 1$ \citep{Goh}, red circles correspond to a fixed vector $\mathbf{r_i} = 1 \ \forall \ i$ (Goh and Jennings 1977), blue triangles correspond to feasible vectors $\mathbf{r_f}$ chosen randomly inside the feasibility domain, and green stars correspond to the vector $\mathbf{r_c}$ located at the centroid of the feasibility domain. Probabilities are calculated from ten thousand simulations, and the error bars represent the 95% confidence region (calculated as the product of the standard error of the mean and the confidence interval multiplier). Qualitative results are robust to the change of parameter values and sampling distributions (see Appendix S1).

feasible communities under a low level of complexity, but as soon as the complexity increases, the probability drops as a function of community size. Similarly, the random vector (gray squares) generated a vast majority of unfeasible communities, confirming previous results shown in Fig. 1. Note that the probability of feasibility derived from the random vectors (gray squares) is a proxy for the average size of the feasibility domain $D_F(\mathbf{A})$. Thus, this probability can be taken as an illustration of how the feasible parameter space of randomly-assembled communities shrinks as a function of community size and complexity (Grilli et al. 2017).

Second, we demonstrated that the sampling of intrinsic growth rates does influence the stability properties of small randomly-assembled communities. Across the different levels of community size and complexity, Fig. 3d–f shows that the feasible vectors $\mathbf{r_f}$ (blue triangles) always have a larger or equal probability of stability than the random vectors (gray squares). Similarly, the centroid vectors $\mathbf{r_c}$ (green stars) and the fixed vectors (red circles) also display on average a higher probability of stability than the

random vectors, revealing that feasibility can impose a stabilizing effect on ecological communities regardless of the specific parameterization. Recall that random vectors yield a majority of unfeasible communities. These results also confirm that under high levels of complexity (above May's stability threshold) the probability of stability decreases as the number of species grows.

Third, we found that not all small feasible randomly-assembled communities are stable, even under a low level of community complexity. Fig. 4a–c shows the probability of local stability for the randomly-assembled feasible communities only. Across the different levels of community size and complexity, these panels show that the probability of stability generated by the feasible vectors $\mathbf{r_f}$ (blue triangles) can, in fact, be significantly less than one. This is a clear example showing that feasibility does not always guarantee the stability of small randomly-assembled communities.

Fourth, we found that specific parameterizations of intrinsic growth rates inside the feasibility domain can lead to larger probabilities of stability. Fig. 4a–c shows
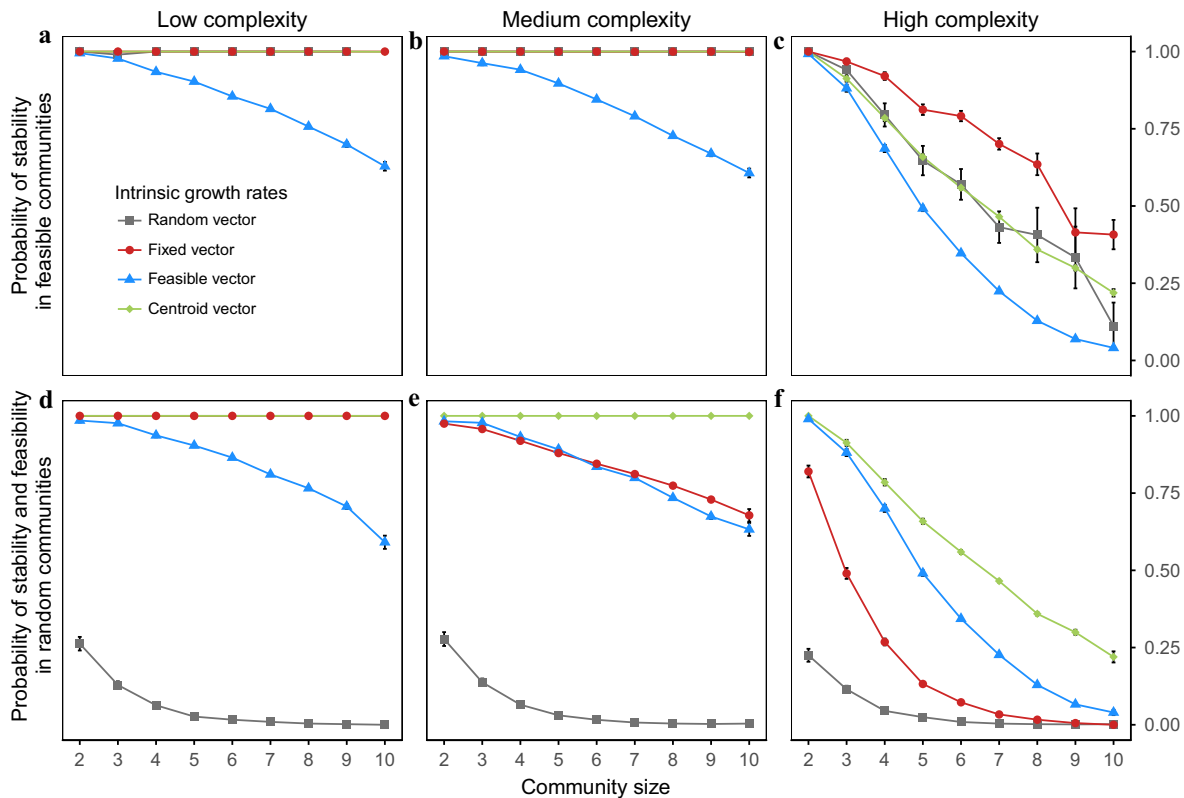

Fig. 4. The choice of parameterization of intrinsic growth rates determines the probability of feasibility and stability in small randomly assembled communities. For different parameterizations of intrinsic growth rates, panels a–c show the probability of stability in feasible randomly-assembled communities only (similar to Fig. 1a) as a function of both the level of community size and complexity. Note that random vectors are generated by sampling randomly and uniformly values in [−1, 1], and do not correspond to an exhaustive sampling of all possible vectors. That is, each sampling distribution imposes a different bias that could lead to over or underestimate the probability of stability of feasible communities (blue triangles). Panels d–f show the combined probability of stability and feasibility in randomly-assembled communities. The conditions used to generate randomly-assembled matrices are identical to those specified in Fig. 3. Note that panels d–f here are almost identical to the panels d–f in Fig. 3.

that focusing on the subset of feasible randomly-assembled communities, the fixed vectors (red circles) and the random vectors (gray squares) can display larger probabilities of stability than the feasible $\mathbf{r_f}$ (blue triangles) and centroid vectors $\mathbf{r_c}$ (green stars). However, recall that the fixed and random vectors correspond to a particular case of parameterization and to a random (and small) subset of feasible communities, respectively. That is, they do not correspond to an exhaustive or representative sample of the feasibility domain. Thus, focusing on a single parameterization or on an arbitrary subset of communities can lead us to either under or overestimate the stability properties of feasible communities (see Appendix S1 for biases on other parameterizations). In fact, we can verify this sampling problem by systematically investigating the combined probability of feasibility and stability in all randomly-assembled communities. Fig. 4d–f shows that the combined probability of feasibility and stability is different for the random and fixed vectors compared to the results obtained with the parameterizations bounded within the feasibility domain.

Finally, we found that stability imposes a filtering of species abundances towards more even distributions in small feasible randomly-assembled communities. Focusing on the vector of intrinsic growth rates located at the centroid of the feasibility domain, Fig. 4d–f shows that this is one of the most stable parameterizations. Recall that this parameterization corresponds to even (or uniform) distributions of abundances (Rohr et al. 2016). In general, for random matrices, there is a probability distribution of stability associated with a given abundance distribution (Rohr et al. 2016). This probability distribution is formed by the different matrix parameterizations. If one considers interaction matrices with a symmetric construction, one should expect to see that the uniform distribution of abundances corresponds to either a local maximum or minimum. Fig. 4d–f shows that this corresponds to a maximum. Similarly, Fig. 5 shows that while is more likely that a feasible (stable or unstable) randomly-assembled community is characterized by an uneven distribution of species abundances, the subset of stable feasible randomly-assembled communities is biased "toward" more even distributions. This reveals that the stability of feasible small randomly-assembled communities is linked to the starting distribution of species abundances.

Discussion

Over the last decades, the application of random matrix theory in ecology has been focused on understanding dynamical stability when the dimension of the community tends to infinity (May 1972, Allesina and Tang 2015, Stone 2016). Our study suggests that random matrix theory could also provide important insights about the ensemble and persistence of ecological communities by shifting the focus from large to small communities. Our results could be particularly relevant to the
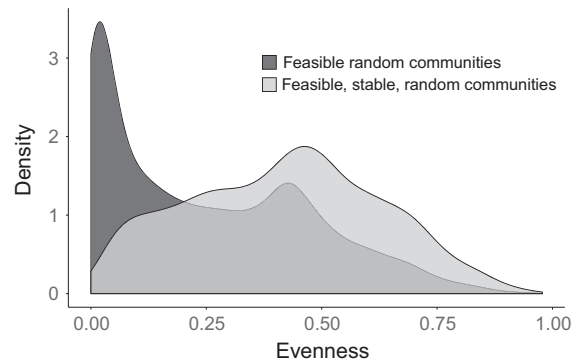

Fig. 5. Link between stability and species abundance distributions. For a randomly-assembled community (as described in the text) with five species, the dark region corresponds to the distribution of evenness over ten thousand random feasible abundances (drawn from a lognormal(0, 5) distribution), and the light region corresponds to the distribution of evenness for the subset that is feasible and stable. Evenness is calculated by the normalized entropy $-\sum_{i=1}^{S} N_i^* \log(N_i^*)/\log(S)$, where $N_i^* \in (0, 1)$ and $\sum_{i=1}^{S} N_i^* = 1$ (see text). Qualitative results are robust to the change of parameter values and community size (see Appendix S1).

understanding of the properties shaping the dynamics of communities during initial successional stages, where interactions are typically unstructured (Odum 1969, Fukami 2015, Saavedra et al. 2017a). Indeed, during initial successional stages, communities are small with high net productivity, high niche specialization, short life cycles, high entropy, species interactions appear to be randomly established (or with no particular pattern), and more vulnerable to external perturbations (Odum 1969, Saavedra et al. 2017a). Importantly, the persistence of these small communities determines the type of environments and opportunities that late-arriving species will face, as species growth may preempt or modify niches substantially before the arrival of late-arriving species (Chase and Leibold 2003, Fukami 2015). This implies that the study of feasibility and stability of small randomly-assembled communities can also shed new light onto the factors driving the composition and properties of larger or mature communities.

In this context, a long-standing and somehow forgotten debate in ecology was whether small randomly-assembled communities can lead to the emergence of feasible and stable communities (Roberts 1974, Goh and Jennings 1977). In particular, whether feasible communities will always be stable or not (Roberts 1974). Capitalizing on recent mathematical tools focused on characterizing the feasibility domain of ecological communities (Rohr et al. 2014, 2016, Saavedra et al. 2014, 2016a,b, 2017b), we have demonstrated that this debate was mainly due to the underestimation of the association of the parameter space of intrinsic growth rates with the feasibility and stability properties of small randomly-assembled communities. We have shown that if one systematically studies the set of vectors of intrinsic growth

rates inside the feasibility domain, the likelihood that a small randomly-assembled community is feasible and stable is not negligible. However, we have found that feasibility does not always guarantee stability. Inside the feasibility domain, it is also possible to find vectors of intrinsic growth rates that are unstable. These properties can be different from the ones that have been derived for large random systems (May 1972, Stone 2016), and calls for a more methodological analysis of small randomly-assembled communities. Overall, our results have demonstrated that not all sampling distributions of intrinsic growth rates lead to the same probabilities of stability and feasibility, which could mistakenly lead to under or overestimate the stability properties of feasible communities (James et al. 2012, Coyte et al. 2015, Wootton and Stouffer 2016).

Our findings have also revealed that there are certain parameterizations of intrinsic growth rates inside the feasibility domain that could lead to a higher probability of stability. For example, under the random parameterization of interaction matrices followed in this study, the vector of intrinsic growth rates located at the centroid of the feasibility domain displays the largest probability of stability among all the parameterizations of intrinsic growth rates. For these randomly-assembled communities, this centroid corresponds to the case where the interaction matrix is proportional to the Jacobian matrix, and represents the most optimistic case of stability for small randomly-assembled communities under LV dynamics. We should stress that these results do not necessarily imply that one should observe a stable uniform abundance distribution more often in small randomly-assembled communities. Recall that the observed abundance distribution is the joint distribution of two independent probability distributions: the probability distribution of abundance distributions in the initial random assembly, and the probability distribution of feasibility and stability for a fixed abundance distribution. Then, the observed abundance distribution of feasible, stable, randomly-assembled communities should be the result of the joint probability. In fact, taking into account all feasible (stable and unstable) randomly-assembled communities, our results show that randomly-assembled communities are very likely to be characterized by uneven abundance distributions (Locey and White 2013). However, focusing on the subset of stable, feasible, randomly-assembled communities, our results do imply that stability imposes a filtering towards more even distributions. Thus, this indicates that the stability of feasible communities is inherently linked to the starting distribution of species abundance, a characteristic that many times has been ignored (Neutel et al. 2007), but should be incorporated in manageable lab and field experiments.

Finally, it is worth recalling that the parameterizations given by the fixed vectors and the centroid vectors should not be considered as a product of a random process, both parameterizations are by construction dependent on all the species present in the community. These parameterizations, however, can be used as potential benchmarks. For example, while the centroid does represent the vector with the largest tolerance to external random perturbations (before leaving the feasibility domain), it should only be advantageous for a randomly-assembled community if perturbations to intrinsic growth rates do occur randomly with no preferred direction (Song et al. 2017, Cenci et al. 2018). All in all, our study highlights that the feasibility and stability of small randomly-assembled communities is the outcome of the combination between the structure of interaction matrices and the structure of the vector of intrinsic growth rates, which together are linked to species abundances. We urged that this combination must not be overlooked if theoretical and empirical studies aim to derive general conclusions about the dynamics and persistence of ecological communities.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2125/suppinfo

DATA ACCESSIBILITY

The R-code supporting the results is archived in Dryad Digital Repository https://doi.org/10.5061/dryad.q104g (Song et al. 2017).