The stability of Lotka-Volterra metacommunities on random dispersal networks*

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Abstract

We study the comparative linear stability of Lotka-Volterra metacommunities in cases where dispersal coefficients between individual communities within the larger metacommunity are either uniformly or normally distributed. We also vary the mean interaction strength between species within a community. In the case of uniform dispersal coefficients, stability (as quantified by the leading eigenvalue of the linearized metacommunity steady state) increases with both number of species S and number of nodes N in the metacommunity when mean interaction strength is low. When mean interaction strength is high we observe decreasing stability with S and N. The rate of change in the leading eigenvalue is higher with respect to N than with respect to S in both high and low mean interaction strength cases. In the case of normally distributed dispersal coefficients, we observe similar behavior with increasing (decreasing) stability for weak (strong) mean interaction strength as a function of S and N. However, the relative rate of change in the leading eigenvalue with respect to S is relatively weak for normally distributed dispersal, relative to uniformly distributed dispersal, which may imply that stability of normally dispersing metacommunities is less sensitive to species loss or gain than uniformly dispersing metacommunities. This result would have broad implications for our understanding of metacommunity spatial dynamics and the role of connectivity between environments.

Introduction

Communities are formed when groups of individuals, populations, or species interact locally in space and time to form a larger cohesive unit governed by the interactions among groups. The dynamics of communities are central to many fields of science, including population and ecosystem ecology, epidemiology, economics, and social science. For example, understanding the conditions under which subunits of a larger organization are able to coexist, destabilize, or promote/demote growth are all important scientific questions addressed as problems in community dynamics.

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Perhaps the most fundamental contribution to the field of community dynamics came from Sir Robert May who studied systems of interacting species from the ecological perspective. May famously showed that general assumptions about the steady state of a community dynamics model led to a negative relation between community complexity (# of species in a community) and the linear stability of those steady states [May, 1972, May, 1973]. Since May, community stability theory has been a cornerstone of theoretical ecology with many important extensions. Most notably, community stability theory has been developed via random matrix theory [Allesina and Tang, 2012, Allesina and Tang, 2015] which considers the general case where particular elements of the interaction matrix may be unknown, but the general structure of the community can be specified by statistical assumptions about matrix elements. For example, one celebrated result from random matrix theory applied to community dynamics is the so-called circular law

$$\sigma\sqrt{SC} < 1$$

which states that a community composed of randomly sampled coefficients will be stable with probability approaching one if the product of the standard deviation of interaction coefficients and the square root of the number of species times the proportion of species that interact is less than one. Another interesting result from community stability theory is from [McCann et al., 1998] who found that communities with heavy tailed interaction coefficient distributions composed of 'many strong and a few weak' interactions promoted stability among a broad class of probabilistic community structures.

The generalization to metacommunities

An important recent extension of community stability was studied by [Mougi and Kondoh, 2016] who considered the metacommunity generalization of May's results. In a metacommunity, individual communities are nested as a node within a dispersal network with flows of species among nodes. In [Mougi and Kondoh, 2016], a uniform probability distribution was assumed for both the magnitude of dispersal flows and for the interaction coefficients between species on a node. In this paper we examine the importance of the dispersal coefficient distribution for metacommunity stability. We also consider the role of mean interaction strength between species within individual communities. In particular, we compare metacommunity stability in the cases where interaction coefficients are uniformly distributed (as in [Mougi and Kondoh, 2016]), but the dispersal coefficients can be either uniformly or normally distributed. We characterize metacommunity stability as the sign and magnitude of the leading eigenvalue for linearized perturbations about the metacommunity steady state. Because the coefficients of the interaction and dispersal matrices are random, we perform Monte Carlo sampling (50 draws per individual experiment) to draw random matrices from the coefficient distributions and compute mean statistics with respect to the eigenvalues of the linearized systems, as explained below.

Methods

Governing system of ordinary differential equations

Assuming a carrying capacity of unity for all species in a community ($K = 1$), the ODE for the time evolution of an individual species concentration x_i in a single Lotka-Volterra community is

$$\dot{x}_i = x_i + x_i \sum_j a_{ij} x_j$$

where the over-dot represents the time-derivative $\frac{d}{dt}$, a_{ij} is the interaction coefficient representing the proportional effect of species j on species i, with the sum taken over all species in the local community. If the community experiences immigration and emigration across communities in a larger metacommunity such that species x_i at a node l experiences a flow of species x_i from node k, we modify the equation to read

$$\dot{x}_i^l = x_i^l + x_i^l \sum_{j \in l} a_{ij}^l x_j + \sum_k m^{lk}(x_i^l - x_i^k)$$

where we now refer to interactions with species j on local node l (i.e. only species on the same node interact), and we include terms representing immigration dispersal from all k alternate nodes ($k \neq l$) with dispersal rate m^{lk}. We write the equation in terms of the difference in concentrations of species i on node l and node k because the dispersal rate from l to k is the same as the rate from k to l. To better understand the network structure of the metacommunity, we note the particular form of the interaction and dispersal matrices. With species arranged in a vector as follows

$$\mathbf{x} = [x_1^1, x_2^1, \ldots, x_S^1, x_1^2, x_2^2, \ldots, x_S^N]$$

matrices $\mathbf{A}$ and $\mathbf{M}$ take on the particular forms

$$\mathbf{A} = \left[\begin{array}{c|c|c|c} \mathbf{A}^1 & \mathbf{0} & \ldots & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{A}^2 & \ddots & \vdots \\ \hline \vdots & \ddots & \ddots & \vdots \\ \hline \mathbf{0} & \ldots & \ldots & \mathbf{A}^N \end{array}\right],$$

$$\mathbf{M} = \left[\begin{array}{c|c|c|c} -(N-1)m\mathbf{I} & m\mathbf{I} & \ldots & m\mathbf{I} \\ \hline m\mathbf{I} & -(N-1)m\mathbf{I} & \ddots & \vdots \\ \hline \vdots & \ddots & \ddots & \vdots \\ \hline m\mathbf{I} & \ldots & \ldots & -(N-1)m\mathbf{I} \end{array}\right].$$

Monte Carlo stability analysis

To characterize the stability of a metacommunity, we first find the steady state solutions $\tilde{\mathbf{x}}$ that solve

$$\dot{\mathbf{x}} = \mathbf{0}$$

for $\mathbf{x} = \tilde{\mathbf{x}}$. Small deviations about the steady state $\mathbf{x} = \tilde{\mathbf{x}} + \tilde{\mathbf{x}}'$ are described by the linear equation

$$\dot{\tilde{\mathbf{x}}}' = \mathbf{J}\tilde{\mathbf{x}},$$

where $\mathbf{J}$ is the Jacobian matrix for the metacommunity dynamics, evaluated at steady state

$$j_{ij}^l = \frac{\partial g(x_i^l)}{\partial x_j^l}\bigg|_{\substack{x_i^l = \tilde{x}_i^l \\ x_j^l = \tilde{x}_j^l}}.$$

Following [Mougi and Kondoh, 2016], we specify a uniform distribution for all interaction coefficients. For a generic variable y the functional form for the uniform distribution is

$$U(y, a, b) = \frac{1}{b-a},\ a \leq y \leq b,$$

where values have equal probability on the interval (a, b) and zero probability elsewhere. For dispersal coefficients, the distribution of individual matrix elements can have either a uniform or normal distribution, depending on the combination in question. The functional form for the normal probability density is

$$N(y, \mu, \sigma^2) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(y-\mu)^2}{2\sigma^2}},$$

where μ is the mean and σ^2 is the variance. For both interaction and dispersal coefficients we choose uniform distribution parameters $a = -0.1, b = 0.1$ for the case of weak mean interaction strength ($|\bar{a}| = 0.05$) and $a = -1, b = 1$ for the case of strong mean interaction strength ($|\bar{a}| = 0.5$). For normally distributed dispersal coefficients we chose normal distribution parameters $\mu = 0, \sigma^2 = 0.16$. These parameters were used for both strong and weak interaction strength cases.

Results

In the case of uniformly distributed dispersal coefficients, stability was found to increase with both number of species S and number of nodes N in the metacommunity when mean interaction strength is low ($|\bar{a}| = 0.05$). The average slope in the leading eigenvalue with respect to S for $|\bar{a}| = 0.05$ is approximately $\frac{-0.03}{species}$ (averaging across N), while the slope in leading eigenvalue with respect to N for $|\bar{a}| = 0.05$ was $\frac{-0.05}{node}$ (averaging across S). These slopes are interpreted as the average change in the leading eigenvalue with the addition of one species or one node, respectively. For uniform dispersal coefficients with high mean interaction strength ($|\bar{a}| = 0.5$), we observe decreasing stability with S and N. The average change in the leading eigenvalue with respect to S for $|\bar{a}| = 0.5$ is approximately $\frac{+0.05}{species}$ and $\frac{+0.25}{node}$.

In the case of normally distributed dispersal coefficients, stability similarly increases with both number of species S and number of nodes N in the metacommunity when mean interaction strength is low ($|\bar{a}| = 0.05$). The average slope in the leading eigenvalue with respect to S and N for $|\bar{a}| = 0.05$ is approximately $\frac{-0.01}{species}$ and $\frac{-0.5}{node}$, respectively (after averaging over the values of the alternate variable, as above). For normal dispersal coefficients when mean interaction strength is high ($|\bar{a}| = 0.5$), we observe decreasing stability with S and N, with average slope in the leading eigenvalue of approximately $\frac{+0.01}{species}$ and a slope of the leading eigenvalue with respect to N of approximately $\frac{+0.25}{node}$.

Discussion

The metacommunity generalization of classical community stability theory is an important research program in understanding natural communities characterized by spatial extent and diverse flows of species in space and time. Extending [Mougi and Kondoh, 2016], we investigated the role of functional form for the probability distribution of dispersal coefficients. The finding that the stability of normally dispersing metacommunities is less sensitive to species loss or gain, relative to uniformly dispersing metacommunities, has potentially important consequences for the dynamics of spatial systems.

As dispersal is generated by a variety of processes in natural communities, we expect a wide class of dispersal network structures to be operating in nature. Interesting examples of metacommunity connectivity include aquatic plankton communities experiencing fluid transport, or bacterial communities living on the surface of one's hand experiencing immigration and emigration during a handshake. The distribution of flows on such dispersal networks is a fascinating question and is surely more complicated than the simple distributions considered here. We made restrictive assumptions about the structure of the dispersal network that allowed us to investigate the problem in a preliminary setting. One particularly rigid assumption in this study is that the strength of the dispersal flows do not change over time. Natural metacommunities likely experience variation in the processes transporting species in space which may have a first-order impact on metacommunity stability.

The role of interaction strength is clearly critical in determining metacommunity stability as evidenced by the opposite sign of stability trends with S and N depending on whether a strong or weak mean interaction strength was specified. This result was anticipated from the results of [May, 1972] who showed that an individual random community matrix is stable with probability approaching one if

$$|\bar{a}| < \frac{1}{\sqrt{n}}.$$

The question of whether similar relationships are general to metacommunities across a variety of dispersal structures is an important piece of follow up research.

Another interesting extension to this analysis would involve studying the impulse response of metacommunities about the steady state. In this case we study the pattern of metacommunity response in the metacommunity to specified perturbations of the form $\mathbf{x} = \tilde{\mathbf{x}} + \tilde{\mathbf{x}}'$. In this case we not only look at the rate at which a community regains steady state, but also at the transient response and how the perturbation spreads throughout the metacommunity. The solution for a steady state impulse response has the form

$$\tilde{\mathbf{x}}'(t) = c_1 e^{\lambda_1 t}\mathbf{v}_1 + c_2 e^{\lambda_2 t}\mathbf{v}_2 + \cdots + c_q e^{\lambda_q t}\mathbf{v}_q$$

where $c_1, c_2, ..., c_q$ are constants, while $\lambda_1, \lambda_2, ..., \lambda_q$ are the eigenvalues of $\mathbf{J}$ along respective eigenvectors $v_1, v_2, ..., v_q$.

In summary, we find strong motivation to extend our study of metacommunity stability in the context of more diverse dispersal network structures. Preliminary results suggest that some dispersal networks may respond differently to species addition or deletion which is a problem of broad general interest. We hope to extend this research to a more diverse setting to better understand the theory of metacommunities and the factors that help or hinder metacommunity stability.

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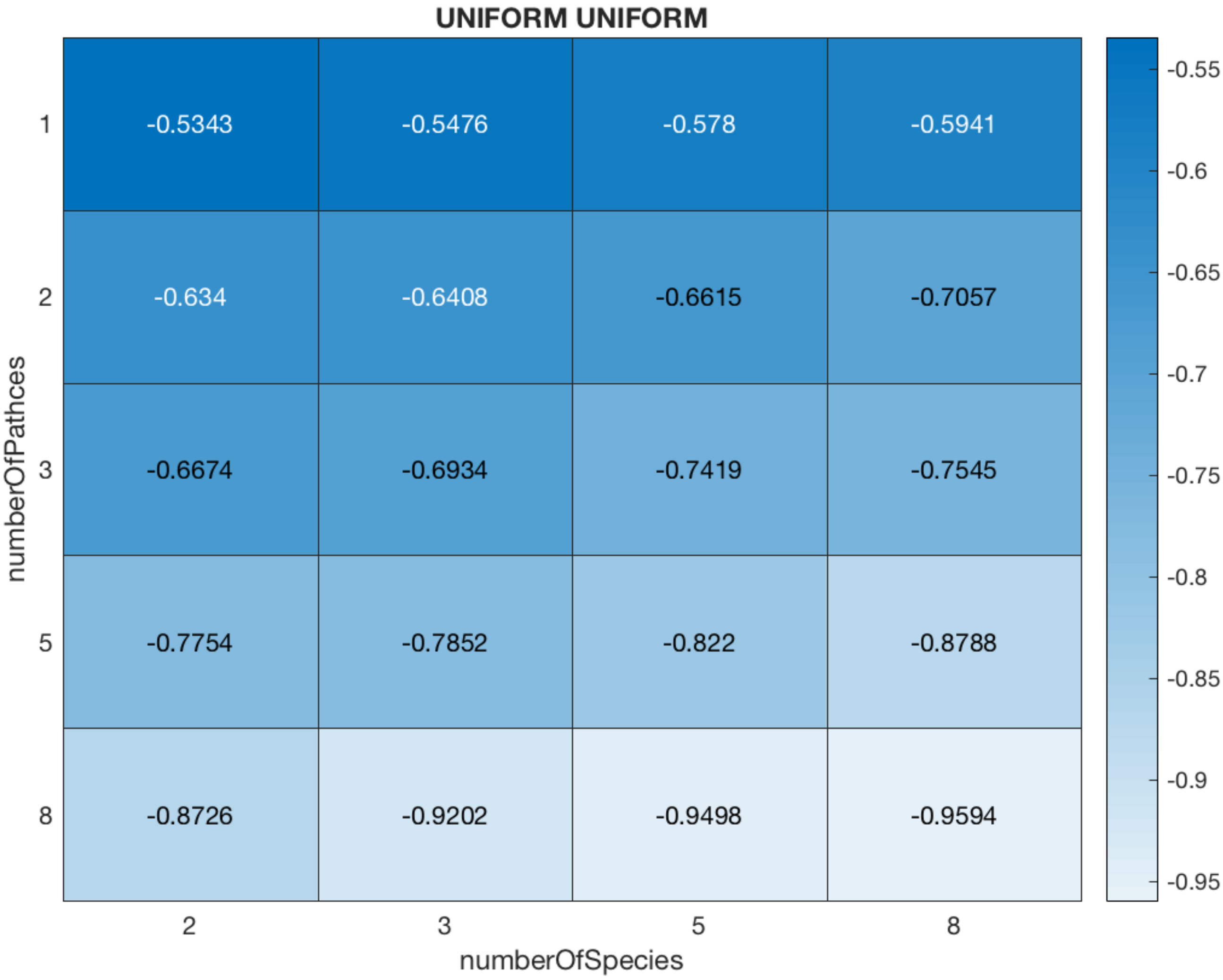

Figure 1: Distribution of the mean leading eigenvalue as a function of number of species S and number of nodes N for the case of uniform interaction coefficients, uniform distributed dispersal coefficients, and weak mean interaction coefficient $|\bar{a}| = 0.05$

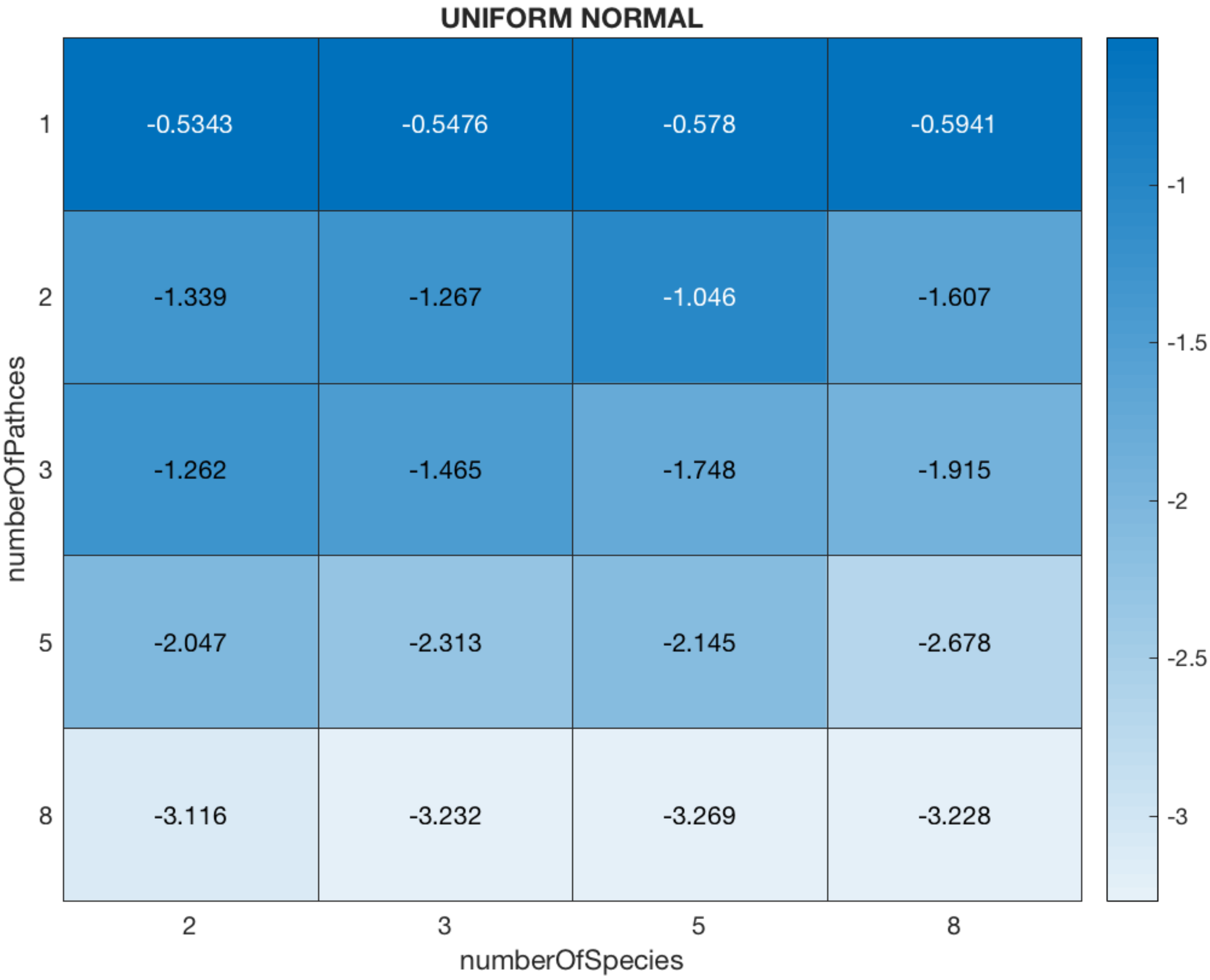

Figure 2: Distribution of the mean leading eigenvalue as a function of number of species S and number of nodes N for the case of uniform interaction coefficients, normally distributed dispersal coefficients, and weak mean interaction coefficient $|\bar{a}| = 0.05$

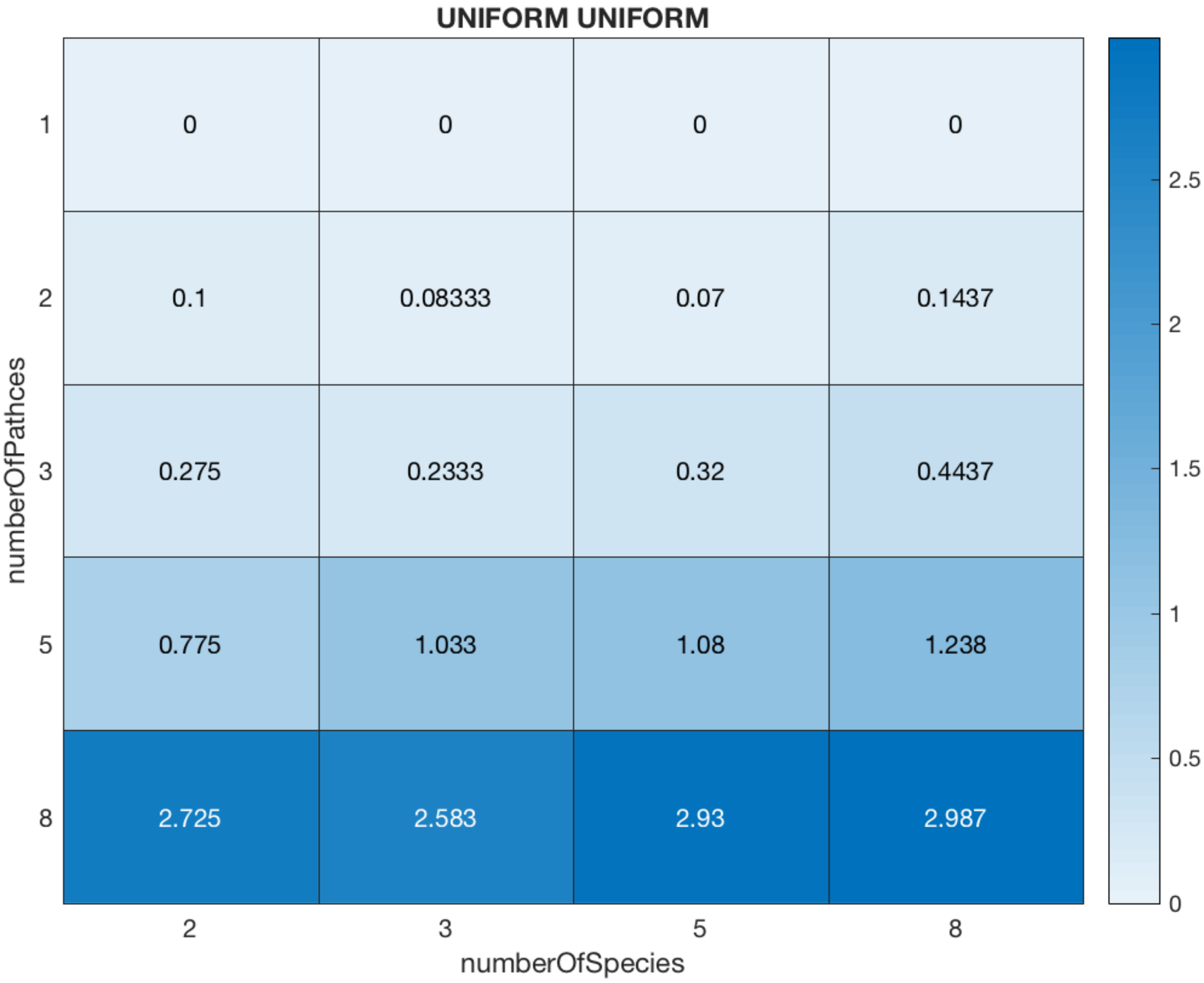

Figure 3: Distribution of the mean leading eigenvalue as a function of number of species S and number of nodes N for the case of uniform interaction coefficients, uniform distributed dispersal coefficients, and strong mean interaction coefficient $|\bar{a}| = 0.5$

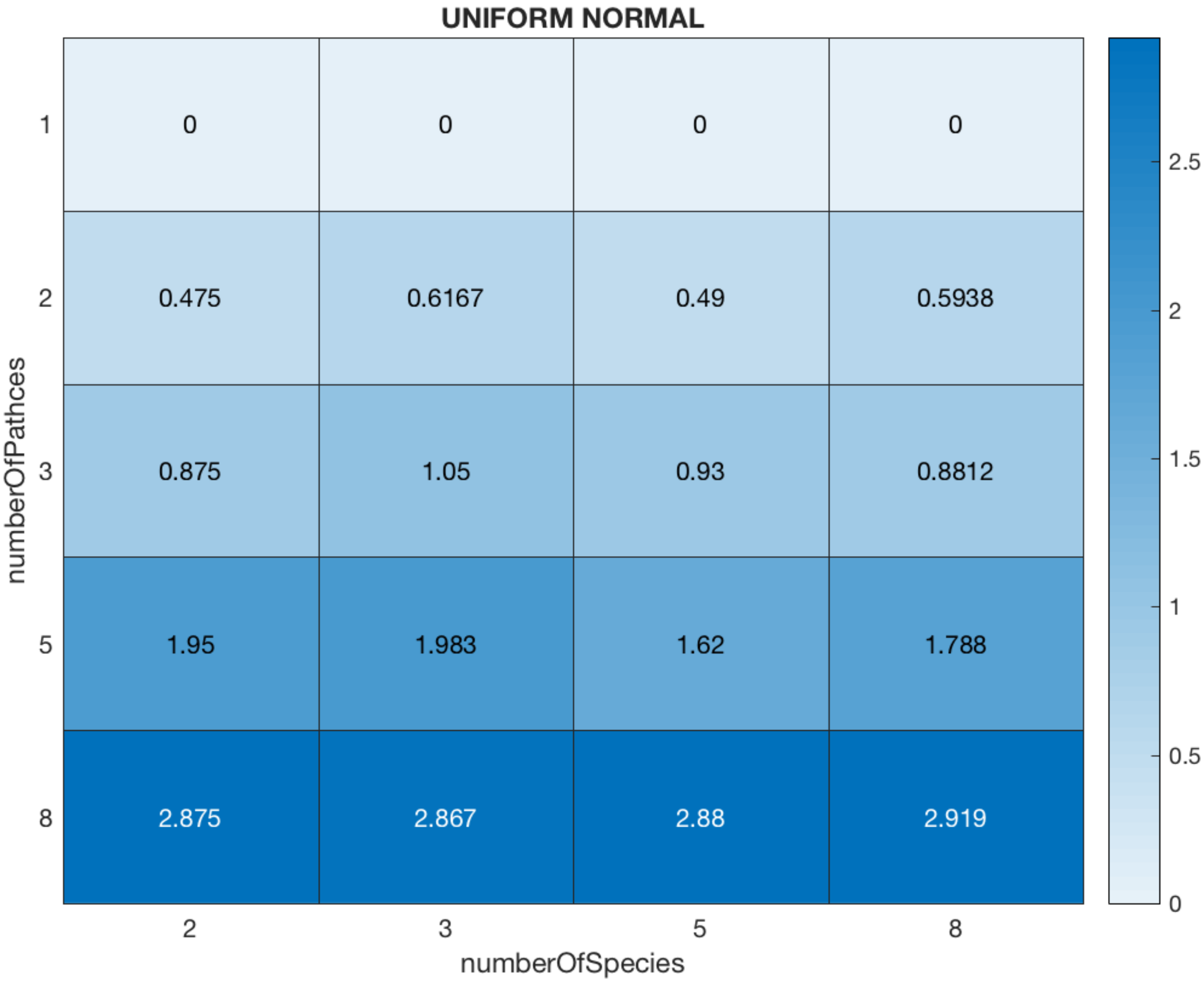

Figure 4: Distribution of the mean leading eigenvalue as a function of number of species S and number of nodes N for the case of uniform interaction coefficients, normally distributed dispersal coefficients, and strong mean interaction coefficient $|\bar{a}| = 0.5$