Trait dimensionality effects on model communities

Carlos A. Serván

Joint work with Z.Miller, J.A. Capitán, T.Bodnar and S. Allesina

Allesina Lab The University of Chicago





Let s_i for i = 1, ..., n be the species at a local community.

Let s_i for i = 1, ..., n be the species at a local community.

$$s_i
ightarrow t_i := egin{pmatrix} t_1^i \ dots \ t_k^i \end{pmatrix} \in \mathcal{T}$$

Let s_i for i = 1, ..., n be the species at a local community.

$$s_i
ightarrow t_i := egin{pmatrix} t_1^i \ dots \ t_k^i \end{pmatrix} \in \mathcal{T}$$

 $g:\mathcal{T}
ightarrow \mathbb{R}$

Let s_i for i = 1, ..., n be the species at a local community.

$$s_i
ightarrow t_i := egin{pmatrix} t_1^i \ dots \ t_k^i \end{pmatrix} \in \mathcal{T}$$

$$g: \mathcal{T} o \mathbb{R}$$

 $f: \mathcal{T} imes \mathcal{T} o \mathbb{R}$

Let s_i for i = 1, ..., n be the species at a local community.

$$s_i
ightarrow t_i := egin{pmatrix} t_1^i \ dots \ t_k^i \end{pmatrix} \in \mathcal{T}$$

$$egin{aligned} g &: \mathcal{T} o \mathbb{R} \ f &: \mathcal{T} imes \mathcal{T} o \mathbb{R} \ f_t &: \mathcal{T} o \mathbb{R}, t' o f(t,t') \end{aligned}$$

Let s_i for i = 1, ..., n be the species at a local community.

$$s_i
ightarrow t_i := egin{pmatrix} t_1^i \ dots \ t_k^i \end{pmatrix} \in \mathcal{T}$$

$$egin{aligned} g &: \mathcal{T} o \mathbb{R} \ f &: \mathcal{T} imes \mathcal{T} o \mathbb{R} \ f_t &: \mathcal{T} o \mathbb{R}, t' o f(t,t') \end{aligned}$$

In our case $\mathcal{T} = \mathbb{R}^k$ and:

$$egin{aligned} g &: \mathcal{T} o \mathbb{R}, t o 1 \ f &: \mathcal{T} imes \mathcal{T} o \mathbb{R}, (t,t') o \langle t,t'
angle \end{aligned}$$

For $x \in \mathbb{R}^n$:

$$\frac{dx}{dt} = x \circ (r - Ax)$$

For $x \in \mathbb{R}^n$:

$$\frac{dx}{dt} = x \circ (r - Ax)$$

$$r = 1$$

$$A_{ij} = \frac{1}{k}f(t_i, t_j)$$

$$G = [t_{ji}] \in \mathbb{R}^{k \times r}$$

$$A = \frac{1}{k}G^T G$$

(Thm 15.3.1 Hofabuer and Sigmund 1998) Since A is symmetric and positive definite $(k \ge n)$ we have a unique globally stable fixed point parameterized by $S \subset N = \{1, ..., n\}$:

$$x_i > 0 , i \in S$$
 (Feasibility)
 $x_S(Ax_S + r) = 0$ (Equilibrium)
 $(Ax_S + r)_i < 0 , i \notin S$ (Non-invasibility)

Non-invasible/saturated fixed point



Random zoo

- Jose A. Capitán (Universidad Politécnica de Madrid)
- Jacopo Grilli (ICTP)
- Kent E. Morrison (American Institute of Mathematics)
- Stefano Allesina (Chicago)



(Top Down approach)

- Take a pool of *n* species.
- Let dynamics elapse.
- $k \leq n$ species are coexisting.
- We want to determine P(k|n).
- Study random ecosystems.

(Top Down approach)

- Take a pool of *n* species.
- Let dynamics elapse.
- $k \leq n$ species are coexisting.
- We want to determine P(k|n).
- Study random ecosystems.

(For symmetric stable systems, equivalent to Bottom up approach)

Random Zoo

Computed the distribution of sizes of the survival community for the cases: (A_{ij}) and r_i symmetric about 0 random variables

Random Zoo

Computed the distribution of sizes of the survival community for the cases: (A_{ij}) and r_i symmetric about 0 random variables



Nonzero mean



Necessary condition for non-degenerate equilibrium $k \ge n$.

$$G_i \sim \mathcal{N}(0, \Sigma)$$
 (Gaussian distribution)

Necessary condition for non-degenerate equilibrium $k \ge n$.

 $G_i \sim \mathcal{N}(0, \Sigma)$ (Gaussian distribution) $A \sim \mathcal{W}_n(\frac{1}{k}\Sigma, k)$ (Wishart Distribution)

How does the community "look" as a function of the number of traits k?

How does the community "look" as a function of the number of traits k?

- Distribution of the number of survivals : $\mathbb{P}(|S||k, n, \Sigma)$
- Mean number of survivals : $\wp(k, n, \Sigma)$.
- Total biomass at the attractors : $W(k, n, \Sigma)$.

(Thm 15.3.1 Hofabuer and Sigmund 1998) Since A is symmetric and positive definite $(k \ge n)$ we have a unique globally stable fixed point parameterized by $S \subset N = \{1, ..., n\}$:

Probability of feasibility

$$Ax = 1$$
$$x_i > 0$$

$$Ax = 1$$
$$x_i > 0$$

Let $A \sim W_n(\Sigma, k)$, $1_n \in \mathbb{R}^n$ a vector of ones and $L_{n-1} = (I_{n-1}0)$, then (Proof of Thm 1. Bodnar and Okhrin 2011)

$$Ax = 1$$
$$x_i > 0$$

Let $A \sim W_n(\Sigma, k)$, $1_n \in \mathbb{R}^n$ a vector of ones and $L_{n-1} = (I_{n-1}0)$, then (Proof of Thm 1. Bodnar and Okhrin 2011)

$$\tilde{x} = \frac{L_{n-1}A^{-1}\mathbf{1}_n}{\mathbf{1}_n^T A^{-1}\mathbf{1}_n}$$

$$Ax = 1$$
$$x_i > 0$$

Let $A \sim W_n(\Sigma, k)$, $1_n \in \mathbb{R}^n$ a vector of ones and $L_{n-1} = (I_{n-1}0)$, then (Proof of Thm 1. Bodnar and Okhrin 2011)

$$\begin{split} \tilde{x} &= \frac{L_{n-1}A^{-1}\mathbf{1}_n}{\mathbf{1}_n^T A^{-1}\mathbf{1}_n} \\ \tilde{x} &\sim t_{n-1}(k-n+2; \frac{L_{n-1}\Sigma^{-1}\mathbf{1}_n}{\mathbf{1}_n^T \Sigma^{-1}\mathbf{1}_n}, \frac{1}{(k-n+2)\mathbf{1}_n^T \Sigma^{-1}\mathbf{1}_n} L_{n-1}R_1L_{n-1}^T) \end{split}$$

$$Ax = 1$$
$$x_i > 0$$

Let $A \sim W_n(\Sigma, k)$, $1_n \in \mathbb{R}^n$ a vector of ones and $L_{n-1} = (I_{n-1}0)$, then (Proof of Thm 1. Bodnar and Okhrin 2011)

$$\begin{split} \tilde{x} &= \frac{L_{n-1}A^{-1}\mathbf{1}_n}{\mathbf{1}_n^T A^{-1}\mathbf{1}_n} \\ \tilde{x} &\sim t_{n-1}(k-n+2; \frac{L_{n-1}\Sigma^{-1}\mathbf{1}_n}{\mathbf{1}_n^T \Sigma^{-1}\mathbf{1}_n}, \frac{1}{(k-n+2)\mathbf{1}_n^T \Sigma^{-1}\mathbf{1}_n} L_{n-1}R_1L_{n-1}^T) \\ R_1 &= \Sigma^{-1} - \Sigma^{-1}\mathbf{1}_n\mathbf{1}_n^T \Sigma^{-1}/\mathbf{1}_n^T \Sigma^{-1}\mathbf{1}_n \end{split}$$

Probability of feasibility

$$P_f(n) = \int_{\mathbb{R}^{n-1}} d\tilde{x}^{n-1} p(\tilde{x}) \Theta(1 - \mathbf{1}_{n-1}^T \tilde{x}) \prod_i \Theta(\tilde{x}_i)$$

Probability of feasibility

$$P_f(n) = \int_{\mathbb{R}^{n-1}} d\tilde{x}^{n-1} p(\tilde{x}) \Theta(1 - \mathbf{1}_{n-1}^T \tilde{x}) \prod_i \Theta(\tilde{x}_i)$$
$$P_f(n) = \int_{\mathbb{R}} dug(u) \mathbb{P}(y_u \succ 0, \mathbf{1}_{n-1}^T y_u < 1)$$
(1)

Where:

$$u \sim \chi^{2}_{k-n+2}$$

$$y_{u} \sim \mathcal{N}(\frac{L_{n-1}\Sigma^{-1}\mathbf{1}_{n}}{\mathbf{1}_{n}^{T}\Sigma^{-1}\mathbf{1}_{n}}, \frac{1}{u\mathbf{1}_{n}^{T}\Sigma^{-1}\mathbf{1}_{n}}L_{n-1}R_{1}L_{n-1}^{T})$$
(2)

Probability of Non-Invasibility

$$A = \begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix}, \quad \Sigma = \begin{pmatrix} \Sigma_{11} & \Sigma_{12} \\ \Sigma_{21} & \Sigma_{22} \end{pmatrix}$$

Probability of Non-Invasibility

$$A = \begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix}, \quad \Sigma = \begin{pmatrix} \Sigma_{11} & \Sigma_{12} \\ \Sigma_{21} & \Sigma_{22} \end{pmatrix}$$

(Thm 3.2.10 Muirhead 1982):

$$\begin{split} A_{21} | A_{11} &\sim \mathcal{N} \big(\Sigma_{21} \Sigma_{11}^{-1} A_{11}, \Sigma_{22.1} \otimes A_{11} \big) \\ \Sigma_{22.1} &= \Sigma_{22} - \Sigma_{21} \Sigma_{11}^{-1} \Sigma_{12} \end{split}$$

Probability of Non-Invasibility

$$A = \begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix}, \quad \Sigma = \begin{pmatrix} \Sigma_{11} & \Sigma_{12} \\ \Sigma_{21} & \Sigma_{22} \end{pmatrix}$$

(Thm 3.2.10 Muirhead 1982):

$$\begin{split} & A_{21} | A_{11} \sim \mathcal{N} \big(\Sigma_{21} \Sigma_{11}^{-1} A_{11}, \Sigma_{22.1} \otimes A_{11} \big) \\ & \Sigma_{22.1} = \Sigma_{22} - \Sigma_{21} \Sigma_{11}^{-1} \Sigma_{12} \end{split}$$

In particular:

$$A_{21}A_{11}^{-1}1|A_{11} \sim \mathcal{N}(\Sigma_{21}\Sigma_{11}^{-1}1, \mathbf{1}^{\mathsf{T}}A_{11}^{-1}1\Sigma_{22.1})$$

Let $z = 1 - A_{21}A_{11}^{-1}1$, and $W = 1^T A^{-1}1$.

Let
$$z = 1 - A_{21}A_{11}^{-1}1$$
, and $W = 1^T A^{-1}1$.
 $P_{ni}(m) = \mathbb{P}(z \prec 0)$:

Let
$$z = 1 - A_{21}A_{11}^{-1}1$$
, and $W = 1^{T}A^{-1}1$.
 $P_{ni}(m) = \mathbb{P}(z \prec 0)$:
 $P_{ni}(m) = \int_{\mathbb{R}_{+}} dwg(w)O^{-}(n-m, 1 - \Sigma_{21}\Sigma_{11}^{-1}1, w\Sigma_{22.1})$

Theorem 3.2.11 Muirhead 1982 implies that :

$$\frac{1^T \Sigma_{11}^{-1} 1}{W} \sim \chi^2_{k-m+1}$$

Theorem 3.2.11 Muirhead 1982 implies that :

$$\frac{1^T \Sigma_{11}^{-1} 1}{W} \sim \chi_{k-m+1}^2$$

$$P_{ni}(m) = \int_{\mathbb{R}_{+}} dw f(w) O^{-}(n-m, 1-\Sigma_{21}\Sigma_{11}^{-1}1, \frac{1^{T}\Sigma_{11}^{-1}1}{w}\Sigma_{22.1})$$
(3)

For f the density function of χ^2_{k-m+1} .

$$\Sigma = (1 - \rho)I + \rho 11^T$$

$$\Sigma = (1 - \rho)I + \rho \mathbf{1}\mathbf{1}^T$$

$$P_f(n) = \int_{\mathbb{R}_+} dug(u) \frac{-i\sqrt{n\alpha_u}}{\sqrt{2\pi}} \int_{\Gamma} d\zeta e^{\frac{n\zeta^2 \alpha_u}{2}} \Phi(\frac{1/n + \zeta \alpha_u}{\sqrt{\alpha_u}})^n \qquad (4)$$

$$\alpha_u := \frac{1 + (n-1)\rho}{un(1-\rho)}$$
$$\beta_u := \frac{\alpha_u}{n}$$

Constant Correlation $\rho \ge 0$ - Feasibility



$$P_{ni}(m,n) = \int_{\mathbb{R}^+} dw f(w) \int_{\mathbb{R}} dy \phi(y) \Phi(\frac{-1/m + y\sqrt{\beta_w}}{\sqrt{\alpha_w}})^{n-m}$$
(5)
$$\alpha_w = \frac{1 + (m-1)\rho}{mw(1-\rho)}$$
$$\beta_w = \frac{\rho\alpha_w}{1 + (m-1)\rho}$$

$$\mathbb{P}(|S| = m|n, k, \rho) = \binom{n}{m} P_{f,n_i}(m) = \binom{n}{m} P_f(m) P_{ni}(m) = P_a(m) \quad (6)$$

$$\mathbb{P}(|S| = m|n, k, \rho) = \binom{n}{m} P_{f,n_i}(m) = \binom{n}{m} P_f(m) P_{ni}(m) = P_a(m) \quad (6)$$



Approximations for \wp

$$\lambda_q = 1 + \frac{nq\rho}{1-\rho}$$

Approximations for \wp

$$\lambda_{q} = 1 + \frac{nq\rho}{1-\rho} \frac{\gamma - q^{*}}{q^{*}} - (\frac{\phi(\hat{q})}{q^{*}} + \hat{q})((\lambda_{q} - 1)\frac{\phi(\hat{q})}{q^{*}} + \lambda_{q}q^{*}) = 0$$
(7)

Approximations for p

$$\lambda_{q} = 1 + \frac{nq\rho}{1-\rho} \frac{\gamma - q^{*}}{q^{*}} - (\frac{\phi(\hat{q})}{q^{*}} + \hat{q})((\lambda_{q} - 1)\frac{\phi(\hat{q})}{q^{*}} + \lambda_{q}q^{*}) = 0$$
(7)



23

Signature of Trait space dimension



Let T be a rooted phylogenetic tree, with total time 1.

$$\Sigma_{\mathcal{T}}(i,j) = 1 - d(i,j) \tag{8}$$

Let T be a rooted phylogenetic tree, with total time 1.

$$\Sigma_{\mathcal{T}}(i,j) = 1 - d(i,j) \tag{8}$$

In the limit of $\gamma \to \infty$, then $\frac{1}{k}A \to \Sigma_T$.

• Any subset of species coexist (recursive proof)

- Any subset of species coexist (recursive proof)
- The assembly graph is complete

- Any subset of species coexist (recursive proof)
- The assembly graph is complete

What happens in the case of γ *finite*?

Species sorting

(Weber and Agrawal 2014)



Perfectly unbalanced tree



• *k* = *n* is necessary for a non-degenerate equilibrium, but almost never gives full coexistenace.

- *k* = *n* is necessary for a non-degenerate equilibrium, but almost never gives full coexistenace.
- We can detect a signature of the dimension of the trait space (under independent trait values).

- *k* = *n* is necessary for a non-degenerate equilibrium, but almost never gives full coexistenace.
- We can detect a signature of the dimension of the trait space (under independent trait values).
- Our framework reproduces species sorting under phylogenetic correlation.

- Stefano Allesina
- Collaborators: José Capitán, Jacopo Grilli, Kent Morrison, Taras Bodnar, Zachary Miller.
- Angelo Monteiro, Dan Maynard and Matteo Sireci.



Thank you!