Report on current progress on two-species case: competition-colonization trade-off and heteromyopia in 1D-, 2D- and 3D-spaces

Alexey Nikitin[1, a)] and Anton Savostianov[2, b)]

[1)] *Lomonosov Moscow State University, Faculty of Computational Mathematics and Cybernetics*

[2)] *National Research University Higher School of Economics, Faculty of Computer Science*

(Dated: 3 April 2017)

Here we provide the report on the study of dimensionality effects on widely known coexistence mechanisms *competition-colonization trade-off* and *heteromyopia*. As usual we cover general problem statement, describe aforementioned mechanisms towards model's parameter space and show results obtained by developed numerical method. Background on the arising system of non-linear integral equations and numerical method's dimensional heuristics are provided in appendixes.

I. PROBLEM STATEMENT

Assume that we are working with the basic model proposed in [Dieckmann, Law 2000] with following delimitations:

- the population in the scope of the study consists of two species; in words, $i, j, k = 1, 2$;
- no restrictions considered for exogeniuos death rates, thus $d_1 \neq 0$, $d_2 \neq 0$;
- effects of kernel variation are not beyond the scope of the current research; $m_i(\vec{\xi})$ and $w_{ij}(\vec{\xi})$ are distributed normally with zero mathematical expectation;
- in order to get numerical heuristics dispersal and competition kernels are supposed to be radially symmetric (s.t. $f(\vec{\xi}) = f(\|\vec{\xi}\|_2)$, which, we hope, can be treated as biologically reasonable assumption;
- as we show in Appendix B, previous bullet implies radial symmetry for all arising functions, in particular, for second moments $C_{ij}(\xi)$;
- model supposed to be stationary, s.t. all movement events are realized through birth.

Here we put integro-differential equations arising in our model after applying parametric closure:

$$T_{ijk}(\xi, \xi') = \frac{\alpha}{2}\left(\frac{C_{ij}(\xi)C_{ik}(\xi')}{N_i} + \frac{C_{ij}(\xi)C_{jk}(\xi'-\xi)}{N_j} + \right.$$
$$\left. + \frac{C_{ik}(\xi')C_{jk}(\xi'-\xi)}{N_k} - 1\right) + (1-\alpha)\frac{C_{ij}(\xi)C_{ik}(\xi')}{N_i}$$

in system's dynamic equations:

$$\frac{d}{dt}N_i = (b_i - d_i)N_i - \sum_j \int_{\mathbb{R}^n} w_{ij}(\xi)C_{ij}(\xi)d\xi$$

$$\frac{d}{dt}C_{ij}(\xi) = \delta_{ij}m_i(-\xi)N_i + \int_{\mathbb{R}^n} m_i(\xi')C_{ij}(\xi+\xi')d\xi' -$$
$$- d_i C_{ij}(\xi) - \sum_k \int_{\mathbb{R}^n} w_{ik}(\xi')T_{ijk}(\xi,\xi')d\xi - w_{ij}(\xi)C_{ij}(\xi) +$$
$$+ \langle i, j, \xi \to j, i, -\xi \rangle$$

We propose denotations such as $[f * g](\xi) = \int_{\mathbb{R}^n} f(\xi')g(\xi'+\xi)d\xi'$ as classic *convolution* and $y_{ij} = \int_{\mathbb{R}^n} w_{ij}(\xi')C_{ij}(\xi')d\xi'$. Also we use normalized moments $C_{ij} = \frac{C_{ij}}{N_i N_j}$ and $T_{ijk} = \frac{T_{ijk}}{N_i N_j N_k}$ and centralized $D_{ij}(\xi) = C_{ij}(\xi) - 1$.

As we stated earlier, $i, j, k = 1, 2$. We study only physically understandable cases of $n = 1, 2, 3$. As proposed in [Law et al. 2003] we use chosen closure with $\alpha = \frac{2}{5}$.

We study the distribution of the population in equilibium state, s.t.

$$\forall i, j: \ \frac{\partial N_i(t)}{\partial t} = 0, \ \ \frac{\partial C_{ij}(\vec{\xi}, t)}{\partial t} = 0$$

II. MECHANISMS OF CO-EXISTENCE

A. Competition-colonization trade-off

Here we provide some more accurate illustrations for the competition-colonization trade-off which is a widely known mechanism of coexistence; the general rule is that more competitive species can coexist with better dispersed ones. In our study we have found it in $[\sigma_{m2};\ d'_{12}]$ parameter space.

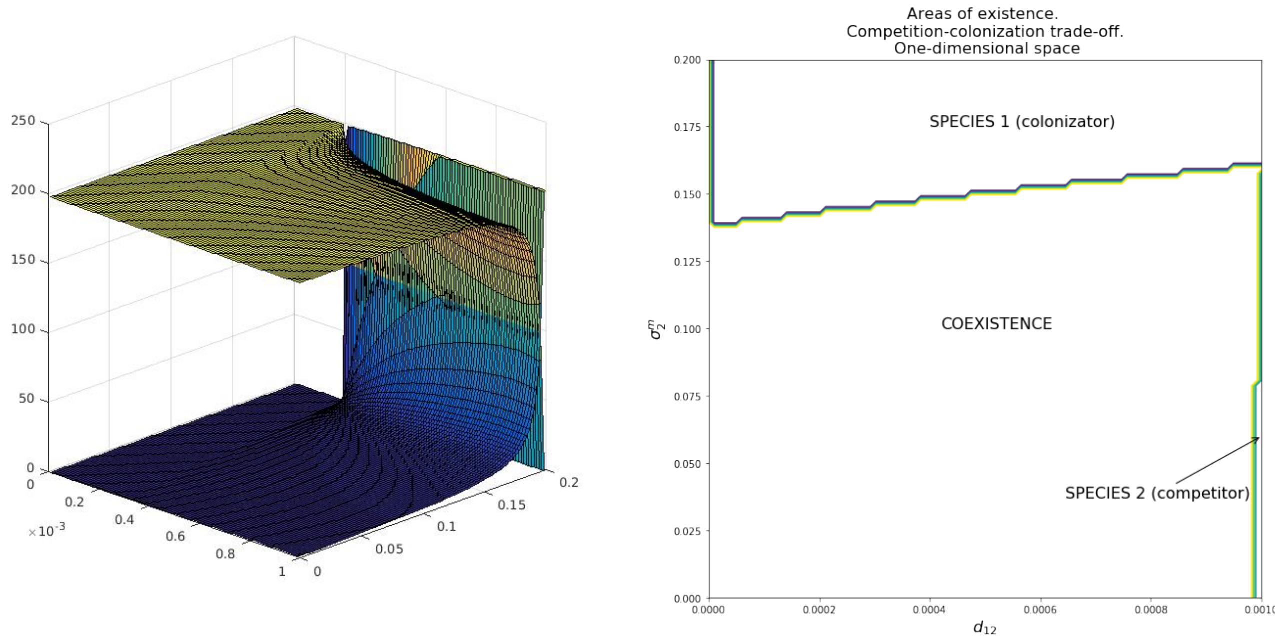
We focus our research on effects of dimensionality for the described mechanism. Figures 1, 2 and 3 are devoted to $\mathbb{R}^1$, $\mathbb{R}^2$ and $\mathbb{R}^3$ respectively. We propose new improved method with fewer mistakes for two-dimensional case and utterly new method for three-dimensional case. For each case we put two subfigures: surfaces of species densities for each pair $(\sigma_2^m; d'_{12})$ and areas in the parameter space that support co-existence or existence of only one species which is denoted by its number on the picture.

We stress out following things regarding obtained results and its further analysis:

- an intreval chosen for d'_{12} should be enlarged in order to obtain greater area of competitor existence;

[a)] nikitin@cs.msu.ru; National Research University Higher School of Economics, Faculty of Computer Science

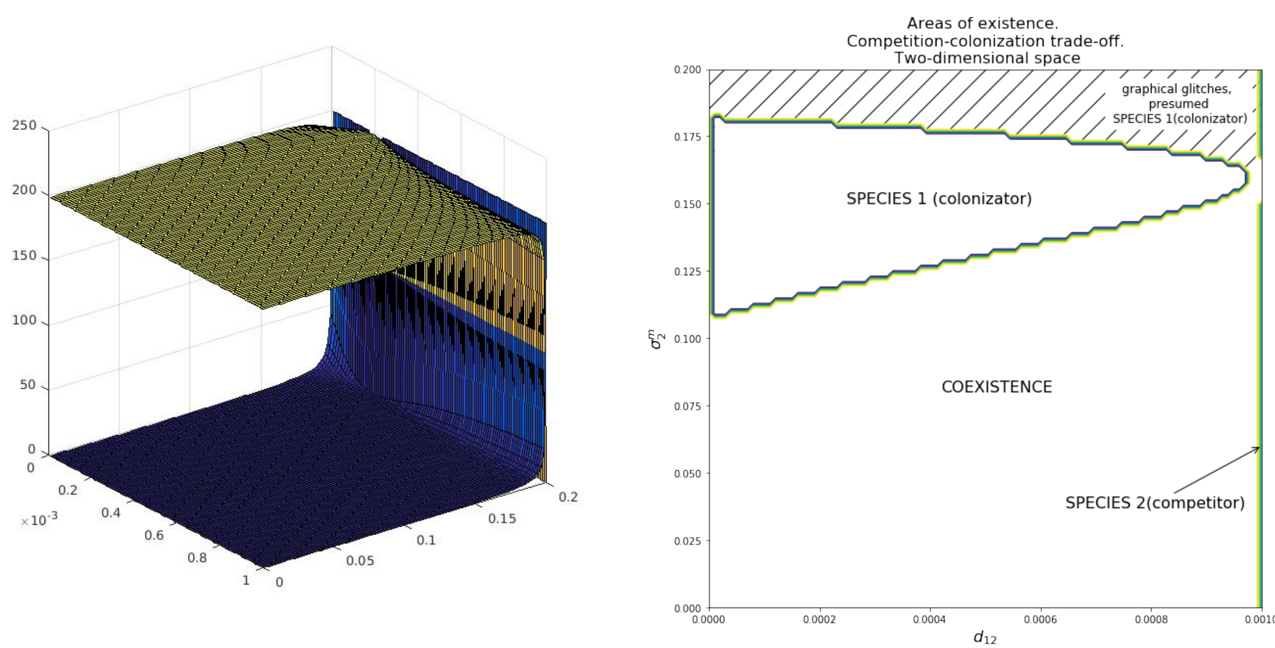
[b)] Electronic mail: a.s.savostyanov@gmail.com



(a) Surfaces of first moment N_1 and N_2 in described parameter space

(b) Areas of coexistence in described parameter space

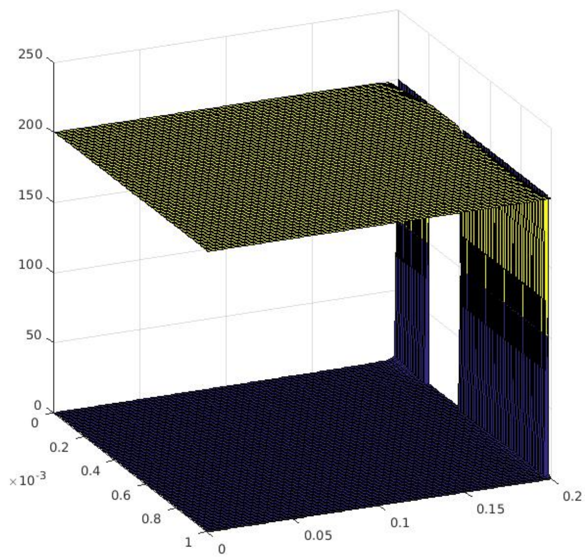
FIG. 1: Realization of Competition-Colonization Trade-Off mechanisms in σ_2^m and d'_{12} parameter space in case of *one-dimensional habitat*. Other parameters are chosen as follows:
$b_1 = b_2 = 0.4, d_1 = d_2 = 0.2, d'_{11} = d'_{22} = d'_{21} = 0.001, \sigma_1^m = 0.04, \sigma_{11}^w = \sigma_{12}^w = \sigma_{21}^w = \sigma_{22}^w = 0.04$



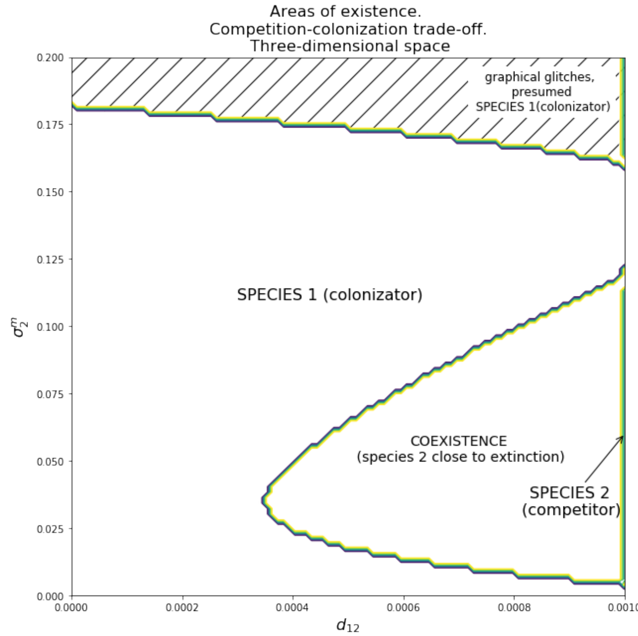
(a) Surfaces of first moment N_1 and N_2 in described parameter space

(b) Areas of coexistence in described parameter space

FIG. 2: Realization of Competition-Colonization Trade-Off mechanims in σ_2^m and d'_{12} parameter space in case of *two-dimensional habitat*. Other parameters are chosen as follows:
$b_1 = b_2 = 0.4, d_1 = d_2 = 0.2, d'_{11} = d'_{22} = d'_{21} = 0.001, \sigma_1^m = 0.04, \sigma_{11}^w = \sigma_{12}^w = \sigma_{21}^w = \sigma_{22}^w = 0.04$



(a) Surfaces of first moment N_1 and N_2 in described parameter space



(b) Areas of coexistence in described parameter space

FIG. 3: Realization of Competition-Colonization Trade-Off mechanisms in σ_2^m and d'_{12} parameter space in case of *three-dimensional habitat.* Other parameters are chosen as follows:
$b_1 = b_2 = 0.4, d_1 = d_2 = 0.2, d'_{11} = d'_{22} = d'_{21} = 0.001, \sigma_1^m = 0.04, \sigma_{11}^w = \sigma_{12}^w = \sigma_{21}^w = \sigma_{22}^w = 0.04$

- the general concept of competition-colonization trade-off holds in all three dimensions; although it should be pointed out that the mechanisms should not be treated as "in order to make species coexist, make one of them overdispersed"; as shown by our figures increase of σ_2^m leads to colonizator domination;

- as the dimensionality of the habitat rises, species-colonizator starts to expel species-competitor: it can be observed that area of the first species enlarges, area of species 2 shrinks and coexistence area moves (two-dimensional case) and shrinks (three-dimensional case);

- in three-dimensional case species 1 practically expels second one; we still can obtain coexistence area, but it should be taken into consideration that in this area density of species 2 is pretty close to 0; in the same time on the right edge of the space this density sharply rises to the state where competitor wins;

- as you may see on figures 2b and 3b that developed numerical method still has number of graphical glitches that are not clearly seen of surfaces' plots; this glitches are supposed to be handled by increasing numerical methods accuracy.

B. Heteromyopia

Here we put our current results for coexistence mechanism called heteromyopia which was proposed in [Murell et al. 2003]. The general principle is that coexistence can be caused in case when interspecies competition radius is larger that intraspecies one. In our model we found this phenomena in space $\left[\sigma_{ii}^w; \sigma_{ij}^w\right]$ which are supposed to be equal (or close to equal).

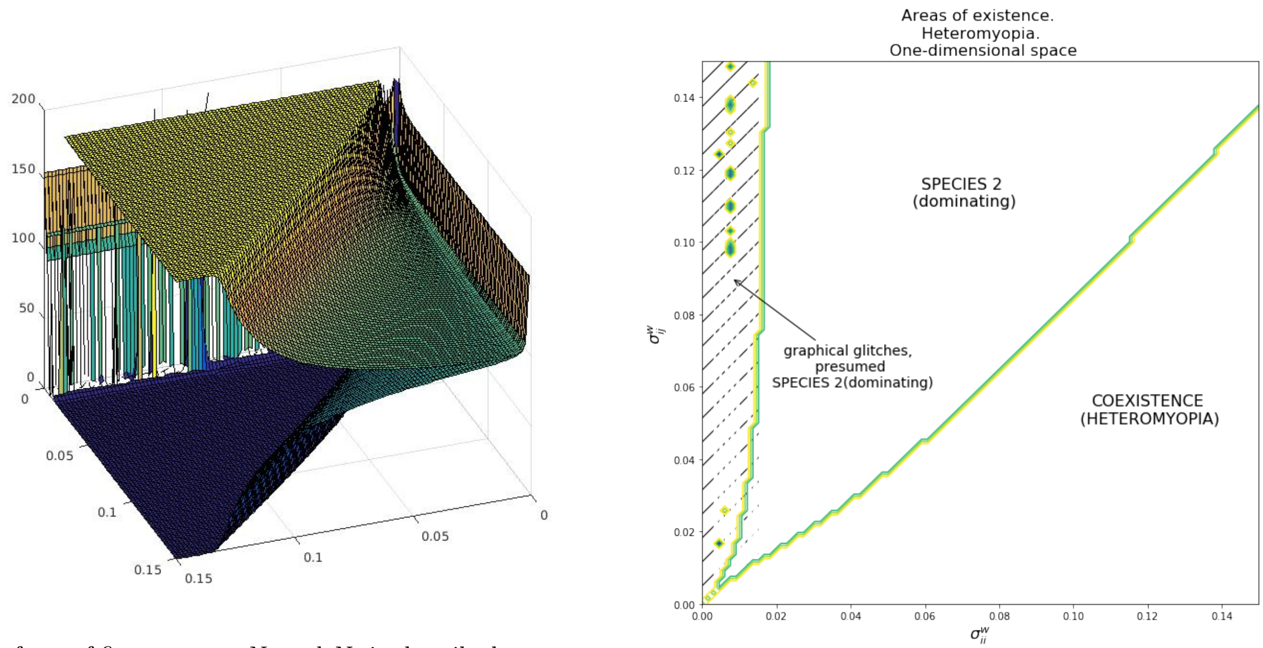
We focus our research on effects of dimensionality for the described mechanism. Figures 4, 5 and 6 are devoted to $\mathbb{R}^1$, $\mathbb{R}^2$ and $\mathbb{R}^3$ respectively. We propose new improved method with fewer mistakes for two-dimensional case and utterly new method for three-dimensional case. For each case we put two subfigures: surfaces of species densities for each pair $(\sigma_{ii}^w; \sigma_{ij}^w)$ and areas in the parameter space that support co-existence or existence of only one species which is denoted by its number on the picture.

We stress out following things regarding obtained results and its further analysis:

- the general concept of the heteromyopia mechanism has been found in one- and three-dimensional cases only; in both cases it is not exactly condition of strict inequality which was proposed in [Murrell et al. 2003] for coexistence arises, but linear approximation is still can be treated as a good call;

- two-dimensional case does not included any pattern similar to heteromyopia that seems to be rather dissapointing;

- as you may see on figures 4b, 5b and 6b that developed numerical method, as on aforementioned pictures for competition-colonization trade-off, has number of graphical glitches; this glitches are supposed to be handled by increasing numerical methods accuracy.



(a) Surfaces of first moment N_1 and N_2 in described parameter space

(b) Areas of coexistence in described parameter space

FIG. 4: Realization of Heteromyopia mechanisms in $\sigma^w_{11} = \sigma^w_{22}$ and $\sigma^w_{12} = \sigma^w_{21}$ parameter space in case of *one-dimensional habitat*. Other parameters are chosen as follows:
$b_1 = b_2 = 0.4, d_1 = d_2 = 0.2, d'_{11} = d'_{22} = d'_{21} = d'_{12} = 0.001, \sigma^m_1 = \sigma^m_2 = 0.06.$

Appendix A: System of equations

Assume the problem stated earlier as follows:

$$\forall i,j: \ \frac{\partial N_i(t)}{\partial t} = 0, \ \ \frac{\partial C_{ij}(\vec{\xi},t)}{\partial t} = 0.$$

System's dynamic equations:

$$\frac{d}{dt}N_i = (b_i - d_i)N_i - \sum_j \int_{\mathbb{R}^n} w_{ij}(\xi)C_{ij}(\xi)d\xi$$

$$\frac{d}{dt}C_{ij}(\xi) = \delta_{ij}m_i(-\xi)N_i + \int_{\mathbb{R}^n} m_i(\xi')C_{ij}(\xi+\xi')d\xi' -$$
$$-d_iC_{ij}(\xi) - \sum_k \int_{\mathbb{R}^n} w_{ik}(\xi')T_{ijk}(\xi,\xi')d\xi - w_{ij}(\xi)C_{ij}(\xi) +$$
$$+\langle i,j,\xi \to j,i,-\xi\rangle$$

We propose denotations such as $[f * g](\xi) = \int_{\mathbb{R}^n} f(\xi')g(\xi'+\xi)d\xi'$ as classic *convolution* and $y_{ij} = \int_{\mathbb{R}^n} w_{ij}(\xi')C_{ij}(\xi')d\xi'$. Also we use normalized moments $C_{ij} = \frac{C_{ij}}{N_iN_j}$ and $T_{ijk} = \frac{T_{ijk}}{N_iN_jN_k}$ and centralized $D_{ij}(\xi) = C_{ij}(\xi) - 1$.

All arising equations should be closed considering:

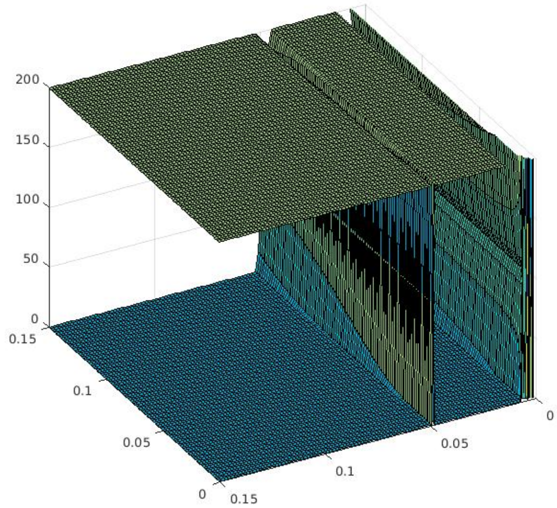
$$T_{ijk}(\xi,\xi') = \frac{\alpha}{2}\left(\frac{C_{ij}(\xi)C_{ik}(\xi')}{N_i} + \frac{C_{ij}(\xi)C_{jk}(\xi'-\xi)}{N_j} + \right.$$
$$\left. + \frac{C_{ik}(\xi')C_{jk}(\xi'-\xi)}{N_k} - 1\right) + (1-\alpha)\frac{C_{ij}(\xi)C_{ik}(\xi')}{N_i}$$

with $\alpha = \frac{2}{5}$.

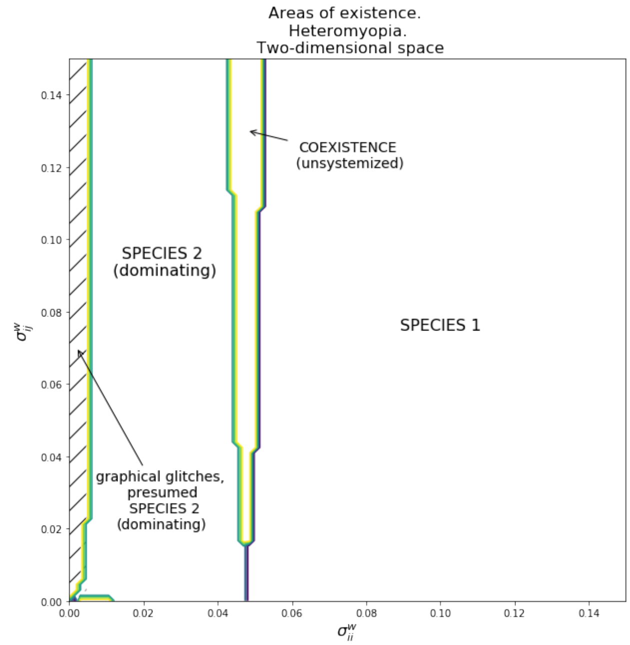
Here we put resulting system:

$$N_1 = \frac{(b_1-d_1)y_{22} - (b_2-d_2)y_{12}}{y_{11}y_{22} - y_{12}y_{21}}$$
$$N_2 = \frac{(b_2-d_2)y_{11} - (b_1-d_1)y_{21}}{y_{11}y_{22} - y_{12}y_{21}}$$

$$((1-\frac{\alpha}{2})b_1 + \frac{\alpha}{2}(d_1 + N_1d'_{11} + N_2d'_{12}) + w_{11})D_{11} = \frac{m_1}{N_1} + [m_1 * D_{11}] - w_{11} -$$
$$-\frac{\alpha}{2}N_1((D_{11}+2)[w_{11} * D_{11}] + [w_{11}D_{11} * D_{11}]) -$$
$$-\frac{\alpha}{2}N_2((D_{11}+2)[w_{12} * D_{12}] + [w_{12}D_{12} * D_{12}])$$



(a) Surfaces of first moment N_1 and N_2 in described parameter space



(b) Areas of coexistence in described parameter space

FIG. 5: Realization of Heteromyopia mechanisms in $\sigma^w_{11} = \sigma^w_{22}$ and $\sigma^w_{12} = \sigma^w_{21}$ parameter space in case of *two-dimensional habitat*. Other parameters are chosen as follows: $b_1 = b_2 = 0.4, d_1 = d_2 = 0.2, d'_{11} = d'_{22} = d'_{21} = d'_{12} = 0.001, \sigma^m_1 = \sigma^m_2 = 0.06.$

$$((1-\frac{\alpha}{2})b_2 + \frac{\alpha}{2}(d_2 + N_1 d'_{21} + N_2 d'_{22}) + w_{22})D_{22} = \frac{m_2}{N_2} + [m_2 * D_{22}] - w_{22} - \\ - \frac{\alpha}{2} N_2((D_{22}+2)[w_{22} * D_{22}] + [w_{22}D_{22} * D_{22}]) - \\ - \frac{\alpha}{2} N_1((D_{22}+2)[w_{21} * D_{12}] + [w_{21}D_{12} * D_{12}])$$

$$((1-\frac{\alpha}{2})(b_1+b_2) + \frac{\alpha}{2}(d_1 + d_2 + d'_{11}N_1 + d'_{12}N_2 + d'_{21}N_1 + d'_{22}N_2) + w_{12} + w_{21})D_{12} = \\ [(m_1+m_2) * D_{12}] - w_{12} - w_{21} - \\ -\frac{\alpha}{2} N_1((D_{12}+2)([w_{11} * D_{12}] + [w_{21} * D_{11}]) + [w_{21}D_{12} * D_{11}] + [w_{11}D_{11} * D_{12}]) - \\ -\frac{\alpha}{2} N_2((D_{12}+2)([w_{12} * D_{22}] + [w_{22} * D_{12}]) + [w_{22}D_{22} * D_{12}] + [w_{12}D_{12} * D_{22}])$$

Appendix B: Heuristics for two- and three-dimensional cases

1. Two-dimensional case

By using ordinary Convolution theorem for $\mathbb{R}^2$:

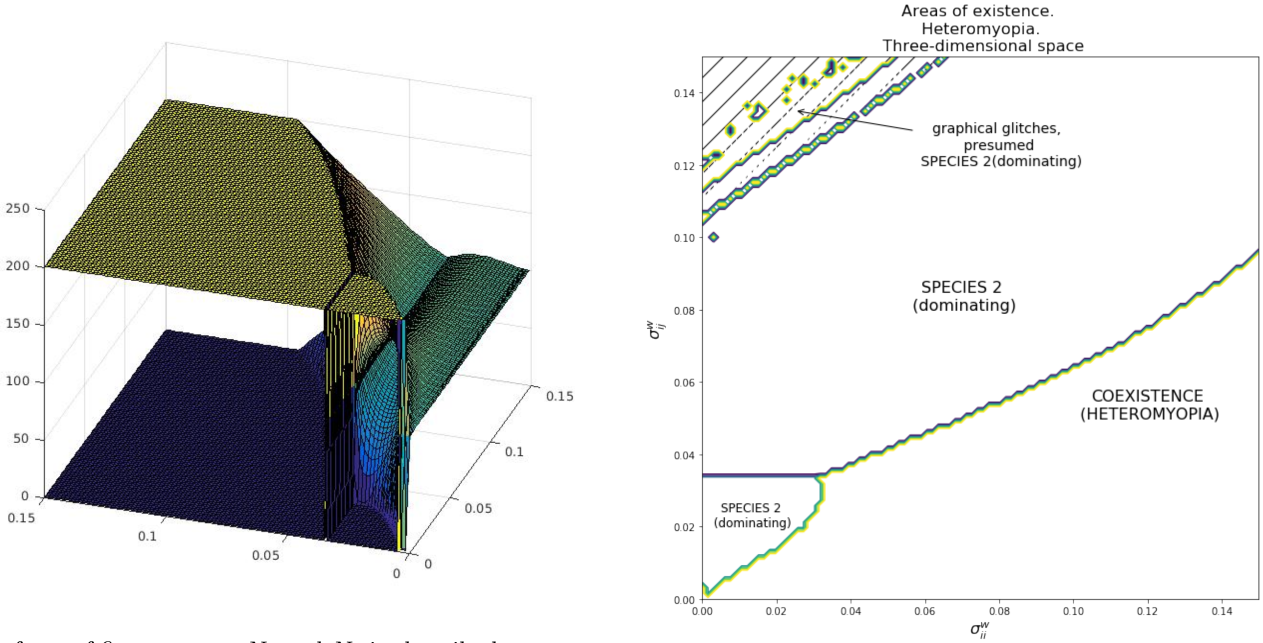
$$[f * *g]_{\mathbb{R}^2} = \hat{F}[F[f] \cdot F[g]]$$

Assume spherical transform:

$$F[f](\omega_x, \omega_y) = \int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty} f(x,y) e^{-i(\omega_x x + \omega_y y)} dx dx y = \\ = \int_{0}^{+\infty}\int_{-\pi}^{\pi} f(r,\theta) e^{-ir\rho\cos(\psi-\theta)} r dr d\theta.$$

By radial symmetry we obtain:

$$F[f](\rho,\psi) = \int_0^{+\infty} r f(r) dr \int_{-\pi}^{\pi} e^{-ir\rho\cos(\psi-\theta)} d\theta$$



(a) Surfaces of first moment N_1 and N_2 in described parameter space

(b) Areas of coexistence in described parameter space

FIG. 6: Realization of Heteromyopia mechanisms in $\sigma^w_{11} = \sigma^w_{22}$ and $\sigma^w_{12} = \sigma^w_{21}$ parameter space in case of *three-dimensional habitat*. Other parameters are chosen as follows: $b_1 = b_2 = 0.4, d_1 = d_2 = 0.2, d'_{11} = d'_{22} = d'_{21} = d'_{12} = 0.001, \sigma^m_1 = \sigma^m_2 = 0.06$.

$$F[f](\rho, \psi) = 2\pi \int\limits_0^{+\infty} r f(r) J_0(r\rho) dr,$$

which is known as Hankell transfrom of the 0-order, where $J_0(x) = \frac{1}{2\pi} \int\limits_{-\pi}^{\pi} e^{-ix\cos\tau} d\tau$ — Bessel function of 0-order and quasi-Convolution theorem can be formulated:

$$H[f * g] = H[(2\pi)^2 H[f] \cdot H[g]]$$

with the same numerical complexity as $[f * g]$.

2. Three-dimensional case

By using ordinary Convolution theorem for $\mathbb{R}^3$:

$$[f *** g]_{\mathbb{R}^3} = \hat{F}[F[f] \cdot F[g]]$$

Treat $F[f]$ as in complex form:

$$F[f] = \int\limits_{\mathbb{R}^3} f(\vec{x}) e^{-i(\vec{w}, \vec{x})} d\vec{x}$$

Assume spherical transform

$$F[f] = \int_0^{+\infty} \int_0^{2\pi} \int_{-\pi/2}^{\pi/2} f(r, \phi, \psi) e^{-i(\vec{w}, \vec{x})} r^2 \sin\psi d\phi d\psi dr$$

By applying Laplass problem on a sphere we obtain the set of orthogonal solutions:

$$y(\phi, \psi) = C_1 \cdot P(\cos\phi) e^{iC_2\psi}$$

where $P(x)$ — Legendre polynome, C_1 and C_2 are constants dependent on order of $P(x)$. Thus we may obtain a spherical harmonics series for $e^{iC_2\psi}$ which can be merged into Fourier transform giving after simplification:

$$[f *** g] = 4\pi[f * g]$$

with the same numerical complexity as [f*g].

Proposed heuristics are only applicable for radially symmetric case. It should be pointed out that this by far proves that this characteristic is invariant for iterative operator used for describing equilibrium points thus we cannot leave a space of radially symmetric functions.

Also we'd like to put that only after proposed heuristics the task of mechanism testing if thorough parameter spaces turned into solvable in reasonable time. In words, coming up with this Appendix was a necessity.