Size-dependent clustering in phytoplankton communities in a 3D environment

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Introduction

Material and methods

Brownian bug model

The Brownian Bug Model (BBM) describes particles going through demographic processes (replication and death) in a turbulent and viscous environment. It has been developed in its 2-dimension, monospecific version in Young *et al.* (2001), which we now extend to 3 dimensions and to multiple species having different demographic and hydrodynamics behaviours. The Brownian Bug Model is a discrete-time, individual-based model where each particle is characterized by its species i and its position $\mathbf{x}^T = (x\,y\,z)$. During each time step of duration τ, events unroll as follow:

1. demography: each particle can either reproduce with probability p (forming a new particle of the sames species i at the same position $\mathbf{x}$), die with probability q, or remain unchanged with probability 1-p-q.

2. diffusion: each particle moves to a new position $\mathbf{x}(t + t') = \mathbf{x}(t) + \delta\mathbf{x}(t)$ where each element of $\delta\mathbf{x}(t)$ follows a Gaussian distribution $\mathcal{N}(0, \Delta)$ with $D = \frac{\Delta^2}{2\tau}$ the diffusivity.

3. turbulence: each particle is displaced by a turbulent flow, following the Pierrrehumbert map (Pierrehumbert, 1994), adapted in its 3D-version (Ngan & Vanneste, 2011).

$$\begin{cases} x(t+\tau) & = x(t+t') + U\tau/2\cos\left(ky(t+t') + \phi(t)\right) \\ y(t+\tau) & = y(t+t') + U\tau/2\cos\left(kz(t+t') + \theta(t)\right) \\ z(t+\tau) & = z(t+t') + U\tau/2\cos\left(kx(t+\tau) + \psi(t)\right) \end{cases}$$

where $U\tau/2$ determines the final velocity of the particle, $k = 2\pi$ and $\phi(t)$, $\theta(t)$, $\psi(t)$ are random phases uniformly distributed between 0 and 2π.

Particles are distributed in a $L \times L \times L$ cube with a volume of 1000 cm^3 for diatoms and 100 cm^3 for nanophytoplankton (volumes are adapted to balance realistic concentrations and computation time) with periodic boundary conditions. Each simulation starts with 10000 uniformly distributed particles and is ran for 1000 timesteps.

Parameter values

We aim at modeling two kinds of communities: diatom-size and nanophytoplankton-size particles (corresponding to indices d and n respectively) to differentiate between the distributions of high-diffusivity and slow-growth particles vs. low-diffusivity and fast-growth particles, respectively. Particles are displaced by a turbulent fluid whose characteristic parameters define the time scale of the whole model: we give here the reasoning behind parameter values, keeping in mind that our model can only be semi-quantitative.

Ecological processes

For both diatoms and nanophytoplankton organisms, $p = \lambda\tau$ and we study the community at equilibrium, i.e. $p = q$. We use a diatom doubling rate of $1d^{-1}$ (Bissinger *et al.*, 2008). We consider the fastest-growing nanophytoplankton particles, corresponding to a diameter of 3 μm (Bec *et al.*, 2008), for which doubling rate is between 2 and 3 d^{-1} (set to 2.5 d^{-1} here).

Advection

We first consider the advection process, due to the turbulence of the environment. From an hydrodynamics point of view, we use the model near Re≈ 1 (Re, Reynolds number).

$$Re = \frac{V L_c}{\nu}$$

where V is the fluid characteristic speed, L_c the characteristic length, and $\nu = 10^{-6}$ m^2/s , the kinematic viscosity for water.

We only consider the Batchelor-Kolmogorov regime, where parent and offspring are separated by a distance lower than k^{-1}, where k is the wavenumber for the flow. Here, we consider the smallest wavenumber corresponding to the largest length scale L, i.e. $k = 2\pi/L$. In this case, we can say

$$
\begin{aligned}
Re &= \frac{U}{k\nu} \\
\Leftrightarrow 1 &= \frac{UL}{2\pi\nu} \\
\Leftrightarrow U &= \frac{2\pi\nu}{L}
\end{aligned}
$$

This means that U=6.3×10^{-4} m.s^{-1}=5.4×10^3 cm.d^{-1}. Using $U\tau/2 = 0.5$ cm as in Young *et al.* (2001), we would have $\tau = 2 \times 10^{-4}$d= 16s.

Diffusion

If we use the Stokes-Einstein equations (Einstein, 1905, cited from Dusenbery, 2009), diffusion can be computed according to the formula:

$$D = \sqrt{\frac{RT}{N_A} \frac{1}{6\pi\eta a}} \tag{1}$$

where $R = 8.314$J.K^{-1}.mol^{-1} is the molar gas constant, $T = 293K$ is the temperature, $N_A = 6.0225 \times 10^{23}$ is Avogadro's number, $\eta = 10^{-3}$m^{-1}.kg.s^{-1} is the viscosity of water and a is the radius of the organism considered. Using $D = \frac{\Delta^2}{2\tau}$,

$$
\begin{aligned}
\Delta &= \sqrt{2\tau D} \\
\Leftrightarrow \Delta &= \sqrt{\frac{RT}{N_A} \frac{\tau}{3\pi\eta a}}
\end{aligned}
$$

Let's apply this formula to organisms of diameter 3μm (see ecological justification below):

$$
\begin{aligned}
< \Delta_n^2 >^{1/2} &= \sqrt{\frac{RT}{N_A} \frac{\tau}{3\pi\eta a}} \\
&= \sqrt{\frac{8.314 \times 293}{6.0225 10^{23}} \frac{1}{3\pi \times 10^{-3} \times 1.5 \times 10^{-6}}} \sqrt{\tau} \\
&= 0.5\sqrt{\tau} \ \mu\text{m}
\end{aligned}
$$

Let's apply this formula to organisms of diameter 50μm (used as a reference in Seymour *et al.*, 2009),

$$
\begin{aligned}
<\Delta_d^2>^{1/2} &= \sqrt{\frac{RT}{N_A}\frac{\tau}{3\pi\eta a}} \\
&= \sqrt{\frac{8.314 \times 293}{6.0225 10^{23}}\frac{1}{3\pi \times 10^{-3} \times 25 \times 10^{-6}}}\sqrt{\tau} \\
&= 0.1\sqrt{\tau}\ \mu m
\end{aligned}
$$

Parameter	Definition	Value
p_d, q_d	Probability of reproducing/dying for diatom particles	$2\,10^{-4}$
p_n, q_n	Probability of reproducing/dying for nanophytoplankton particles	$5\,10^{-4}$
$U\tau/2$	Stretching parameter proxy	0.5 cm
Δ_d	Diffusion parameter for diatoms	5×10^{-5} cm
Δ_n	Diffusion parameter for nanophytoplankton particles	2×10^{-4} cm

Table 1: Definition and value of the main parameters used in the 3D Brownian Bug Model, assuming the duration of a time step τ is 16 seconds.

Metrics

Aggregation and clustering can be quantified by different spatial biodiversity indices (Rajala & Illian, 2012); we focus here on the pair correlation function and the dominance indices. The computation of both indices was checked on known distributions (Poisson and Thomas processes) before being applied to brownian bug model simulations (see Supplementary Material).

Pair correlation function

The pair correlation function (pcf, also written $g(r)$) is a measurement of the aggregation of particles. It can either be computed for a single species (monospecific pair correlation function, $g_{ii}(r)$ for species i) or between species (cross-specific pair correlation function, $g_{ij}(r)$ for species i and j, with $i \neq j$). Let's define C_i and C_j the concentrations of species i and j respectively, and $P_{ij}(r)$ the probability of finding a particle of species i in the sphere dV_1 and a particle of species j in the sphere dV_2 where the centers of dV_1 and dV_2 are serated by distance r.

$$P_{ij}(r) = C_i C_j dV_1 dV_2 g_{ij}(r)$$

When $g_{ij}(r) > 1$, particles are aggregated, and they are segregated when $g_{ij}(r) < 1$.

Computation of the pcf was heavily based on the function `pcf3est` in spatstat 2.2-0 (Baddeley *et al.*, 2015), slightly modified to also compute cross-specific pcf.

Dominance index

The dominance index is presented in (Wiegand *et al.*, 2007). Let $M_{i\bullet}(r)$ be the average number of individuals within a circle of radius r around an individual of species i. $M_{ii}(r)$ corresponds to the conspecific neighbourhood and $M_{io}(r)$ corresponds to individuals of all other species. In this case,

$$d_i(r) = \frac{M_{ii}(r)}{M_{ii}(r) + M_{io}(r)}$$

In case of intraspecific clustering, $d_i(r)$ tends to 1 while it tends to $1/S$, with S the number of species, when the distribution of particles is uniform.

Scale of the study

As we examine particle clustering/segregation and its potential effects on interactions between species, we consider two main processes: direct interactions due to, e.g., competition for nutrients, auxotrophy or allotrophy, and emerging interactions due to predation. Taking direct interactions into account requires to define the volumes of effects surrounding particles, in which they can interact.

Particles with different sizes have different ranges of effects: if we want to consider the effect of clustering on potential interactions between organisms that could be due to auxotrophy, allotrophy, or competition for nutrient at the same location, we need to take these ranges into account. We define nanophytoplankton particles as having a 1.5 μm radius, and their phycosphere radius around 7.5 μm, based on Seymour *et al.* (2009). The maximum distance between two particles of nanophytoplankton is therefore around 15 μm. This corresponds to range of meaningful values between $3\,10^{-4}$ cm and $1.5\,10^{-3}$ cm. We defined diatoms as 50 μm-diameter particles with a corresponding phycosphere of about 1250 μm (Seymour *et al.*, 2009), which means that we can consider radii between $5\,10^{-3}$cm and $2.5\,10^{-1}$ cm.

Predators, on the contrary, are not likely to be restricted by these small phycospheres. We therefore also look at the overall distribution of species, between 10^{-4} and 1 cm , but should keep in mind that processes affecting diversity maintenance are not the same at different scales.
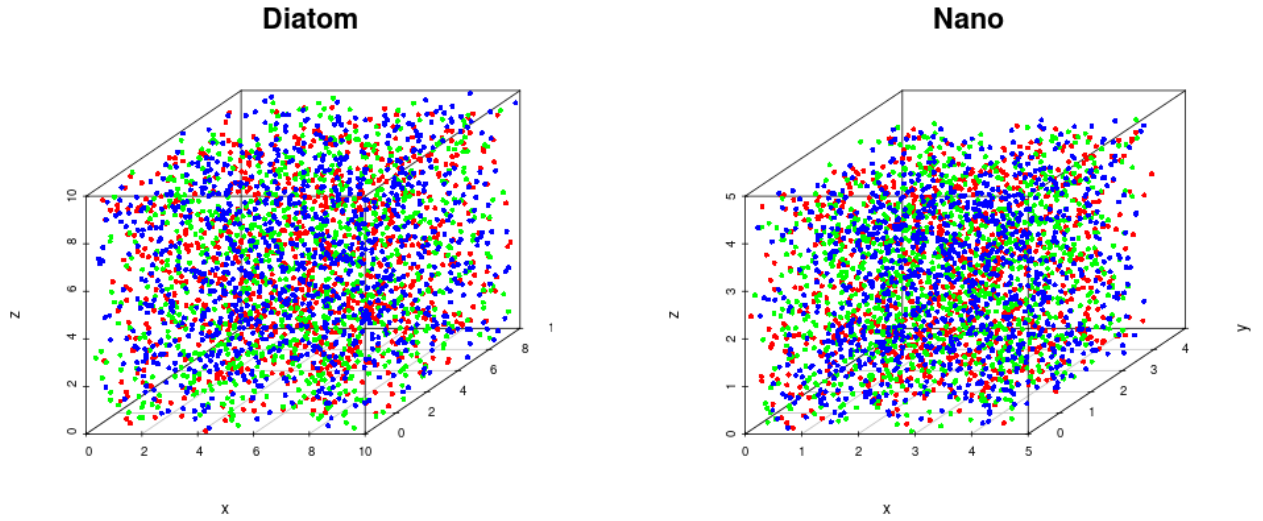
Results

Figure 1: Example of distributions for diatoms and nanophytoplankton after 1000 time steps, starting with 1000 C/L and 10 000 C/L respectively.

We find that particles are strongly clustered, with only small differences between the dominance distributions of diatom and nanophytoplankton-particles (Fig. 2, pcf are shown in the SI).
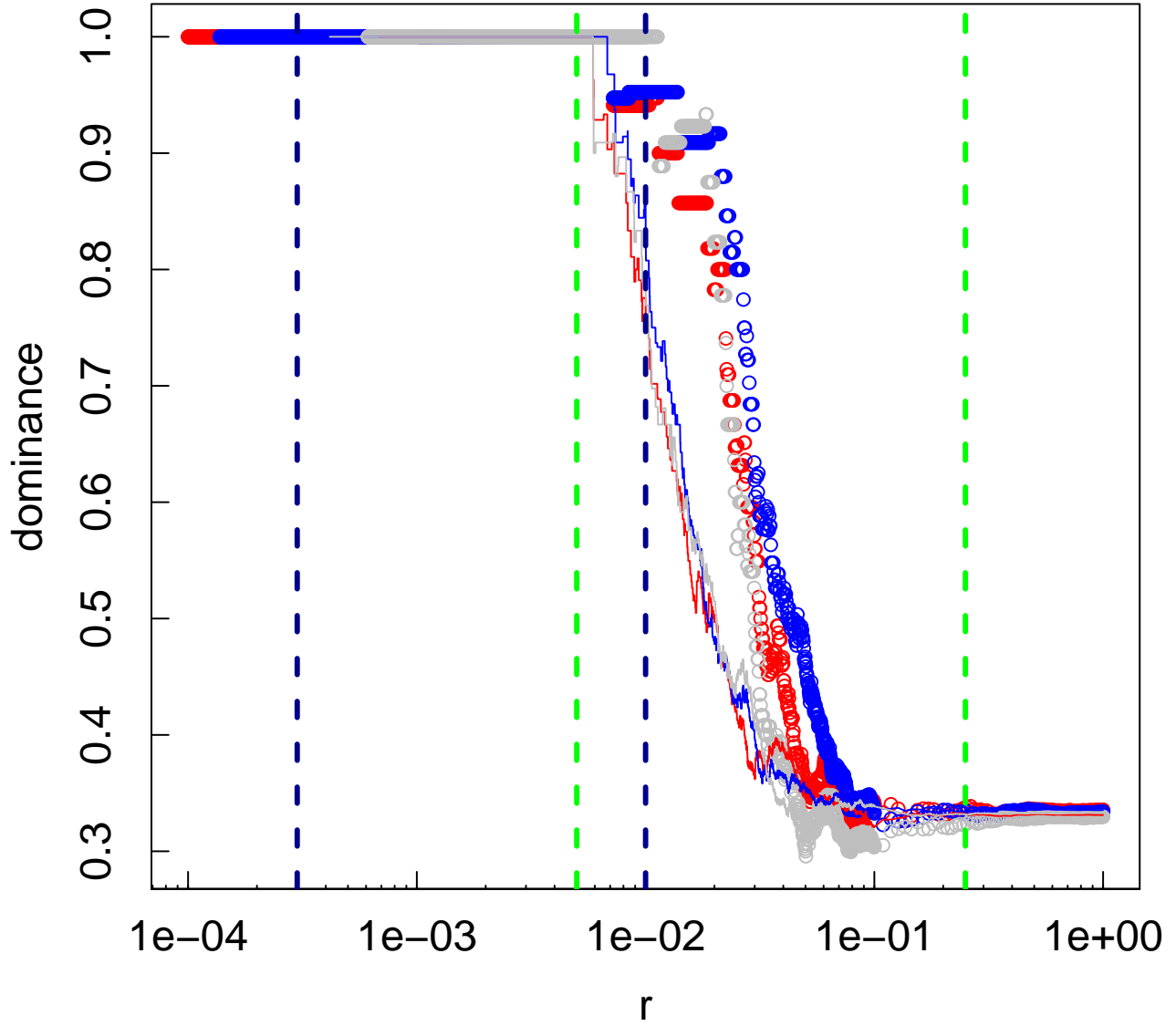
Figure 2: Dominance index for 3 species of diatoms (points) and nanophytoplankton particles (lines) with an even abundance distribution after 1000 time steps. Limits of interactions between particles for diatoms and nanophytoplankton are indicated by green (diatoms) and blue (nanophytoplankton) dashed lines.

Figure 3: Same as above, but for 10 species with a skewed distribution. Simulations are still running.

Discussion

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