AZOI : Another Zone Of Influence model

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AZOI model description

The AZOI model (Another Zone Of Influence) was re-implemented according to the model developed and used by Weiner et al. (2001). The model description follows the ODD protocol for describing individual- and agent-based models (Grimm et al. 2006; Grimm and Railsback 2005) and consists of seven elements. The first three elements provide an overview, the fourth element explains general concepts underlying the model's design, and the remaining three elements provide details.

Purpose

The purpose of the AZOI model is to show the combined effect of competition regime (from total asymmetry to symmetrical share of resources), density and spatial distribution on the sizes and size distributions of plants.

State variables and scales

- The agents of the AZOI model are individual plants represented by their zone of influence (ZOI) where they collect and share areas considered as their primary resource. In this Netlogo implementation, each plant is a turtle and the area is discretely divided in patches.
- As state variables, each plant has its own biomass (`B`), maximum biomass (`Bmax`), optimal growth rate (`r`) and position on the simulated area. Additionally, at each time step the radius of interaction (`rad`) and the effective area (i.e. the ZOI area minus the part lost to neighbors) that each plant can use (`Ae`) are calculated and stored in the parameters of the individuals. The quality of patches can be either qualified in term of ownership to specific plants in the asymmetric competition version, or receive a value of inverse number of competing plant at this patch in the symmetric competition version. In Netlogo:

```
turtles-own[Bmax B r Ae rad …]
```

- The simulation area is 100 by 100 cm, divided in 500 by 500 patches (each patch is thus 0.2cm by 0.2cm, i.e. 0.04cm^2). The area is considered as a torus world (i.e. periodic boundaries). The time step is considered as a growing period and the simulations are usually run for 30 steps.

Process overview and scheduling

As first process of a time step, the patches are assigned a quality depending on the competition submodel (symmetric or asymmetric). The effective area of each plant is then calculated depending on the quality of the patches within its ZOI radius. And finally each plant is grown by an individual-specific rate calculated out of its available effective area and its growth parameters:

```
to go
```

```
    ask patches [set quality to 0]
    ask turtles [set quality of patches in-radius ZOI-radius]
    ask turtles [calculate effective area]
    ask turtles [grow]
end
```

Design concepts

Emergence. – The size distribution of the plants is the major emergent property of the systems modelled by the AZOI model and is dependent on the type of competition regime, density and spatial organization of the individuals.

Adaptation. –

Fitness. –

Prediction. –

Sensing. –

Interaction. – Individual plants interact through overlap of their zones of influences. This interaction determine how well the plant grow on each time step

Stochasticity. – Sizes, growth parameter values and positions (when not regularly installed) of individuals are decided randomly at initialisation.

Collectives. –

Observation. – The biomass of each individual is the most important output and on which are based most of the other observations. A plot of mean biomass through time indicates the general fate of the population depending on the simulation settings. A histogram of number of individuals per biomass classes gives information about the spread and shape of the size distribution. A plot of coefficient of variation of biomass (standard deviation divided by mean) is showing how much variation of biomass occurs and at different time with different simulation settings.

Initialization

The simulations are prepared by first clearing all left-over from previous simulations. The parameters used for hexagonal installation are then eventually calculated. As many plants (turtles) as given by the density input value (Table 1) are then installed randomly or following a hexagonal packing configuration. Each plant receives an initial biomass, maximal biomass and optimal growth rate determined randomly following a normal distribution defined by a mean and standard deviation for each parameter (Table 1).

```
to setup
    clear-all

    […] ; initialize some parameters

    if regular-organization     [ prepare the parameters for hexagonal
                                packing installation]
    create-turtles density [
        set B random-normal Bo-mean Bo-sd
        set Bmax random-normal  Bmax-mean Bmax-sd
        set r random-normal r-mean r-sd
```

```
                    ifelse regular-organization
                            [ hexagonal ]              ; give a position according to
                                                         hexagonal packing
                            [ setxy random-xcor random-ycor ]
                    ]
            […]
    end
```

Input

No inputs are given to the simulations after their initialization.

Submodels

In the Netlogo implementation of the AZOI model, 3 submodels can be distinguished: the growth function, the evaluation of effective area under symmetric competition and the evaluation of effective area under asymmetric competition.

Submodel of growth – The individual at each time steps are growing by a value gr calculated according to the following formula (Weiner et al. 2001):

$$gr = r\left(A_e - \frac{B^2}{B_{\max}^{4/3}}\right)$$

where r is the optimal growth rate (in mg.cm^{-2}.time-step^{-1}), A_e is the effective area of resources that the individual can use which is determined by the competition submodels (see below), B is the actual biomass (in mg) and B_{max} is the asymptotic maximal biomass (in mg). Thus, if $gr > 0$ the next biomass will become $B + gr$.

Submodel of evaluation of effective area under symmetric competition – To calculate the effective area (A_e) under symmetric competition, the logic is to calculate by how many plants each patch are used ($occupants$) and multiply the ZOI area ($B^{2/3}$) by the proportion of shared patches:

$$A_e = B^{2/3} \times \frac{\sum_{patches \in ZOI} \frac{1}{occupants}}{N \text{ of } patches \in ZOI}$$

Thus, the first step is to attribute to each patch the number of individuals sharing this patch. This is done in the AZOI model by asking each plant to add one to the quality of the patches within their radius of ZOI. The second step is to transform these quality values into their inverse. The third step is then to calculate for each plant the number of patches in the ZOI area, and the sum of qualities of patches in the ZOI area, to then be able to proceed with the formula above.

Submodel of evaluation of effective area under asymmetric competition – To calculate the effective area (A_e) under asymmetric competition, the logic is to calculate how many patches each plant can use and multiply the ZOI area ($B^{2/3}$) by the proportion of usable patches:

$$A_e = B^{2/3} \times \frac{N \text{ of usable } patches \in ZOI}{N \text{ of } patches \in ZOI}$$

Thus, the first step is to attribute to each patch the identity value of the individual that will use this patch. This is done in the AZOI model by asking each plant to check the quality of the patches within their radius of ZOI and give this quality their identity value if the other plants trying to use it are smaller. The second step is then to calculate for each plant the number of patches in the ZOI area, and the number of patches in the ZOI area with the quality value equal to the identity of the plant, to then be able to proceed with the formula above.

Reproduction of results

The graphs implemented in the Netlogo version of the AZOI model are showing already several aspects that Weiner et al. (2001) noted with their original model. The easiest result to observe is the mean biomass changing through time and arriving to different values with different competition, density and spatial distribution configurations. The shapes of the distributions are also quite easy to compare among simulation settings and corresponding to what Weiner et al. documented.
With the help of the behavior space analysis it is possible to produce relatively quickly some results showing further comparisons between parameterizations. For example, in figure 1, the biomass distributions are presented as in the histograms of Weiner et al. (with log scale) but at time step = 30 and with three densities. It illustrates the differences among simulation settings in spread of sizes and direction of the skewness. The figure 2 shows the mean coefficient of variation of biomass after 30 time steps (Weiner et al. show the t =10 and 20, but the general results are the same) for the same configurations. It illustrates that asymmetric competition plays a higher role in variation of individual sizes at high density than at low density. The spatial configuration plays also a role, but not as important as the density and regime of competition.

Further analyses

Based on the idea of Stoll et al. (2002) looking at the effect of size symmetry altering biomass-density relationships, the AZOI model was improved to make the individuals die. For this purpose, a threshold of percent of realized growth (realized growth / actual biomass) was used so that individuals with lower realized growth than this threshold were removed. Three different values of threshold were tested (0, 0.2, and 0.5) with a combination of simulation settings using symmetric/asymmetric competition and random/uniform initial installation of plants. The simulations were run with a starting density of 4970 individuals/m^2 and until no individuals were left or up to 200 time steps. The density and mean biomass were recorded at each time step. Linear regression models were fitted for each case with a selection of points where the log-log density-biomass relationship followed a line.

The results of this additional experiment are presented in Fig. 3. The initial installation did not influence the self-thinning trajectory, and only created a faster start of reduction of density with asymmetric competition. Asymmetric competition produced a self-thinning with a critical value of 0% of realized growth while symmetric competition did not. The slopes of the self-thinning trajectories were steeper with asymmetric competition (between -4/3 and -3/2) than with symmetric competition (close to -1). The intercept of the linear models were higher with asymmetric competition than with symmetric one. However, with asymmetric competition, the slopes and intercept of the models were also reduced with higher critical growth threshold.

These results are only partially corresponding to what Stoll et al. (2002) show in their simulation analysis. The general trend of lower intercept with symmetric competition than with asymmetric competition corresponds to what they illustrate with their model and demonstrate with their field experiment. However, they observed similar slopes between the two competition types while the AZOI model presents different ones. Additionally, they attribute all potential changes in self-thinning trajectory to the strength of competition asymmetry but the present quick study demonstrate that the critical threshold value might also play an important role in these trajectories. In biological words, it is not only the capacity to out compete neighbours that determine the overall density-biomass relationship, but also their capacity to cope with harsh growth conditions. Further analyses should enhance these results, although the AZOI model in Netlogo might be a bit slow for full cross checking simulations with hundreds of replicates.

References:

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Weiner, J., P. Stoll, H. Muller-Landau, and A. Jasentuliyana. 2001. The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. The American Naturalist, 158:438-450

Stoll, P., J. Weiner, H. Muller-Landau, E. Müller and T. Hara. 2002. Size symmetry of competition alters biomass–density relationships. Proceedings of the Royal Society, London Series B, 269:2191-2195

Figures

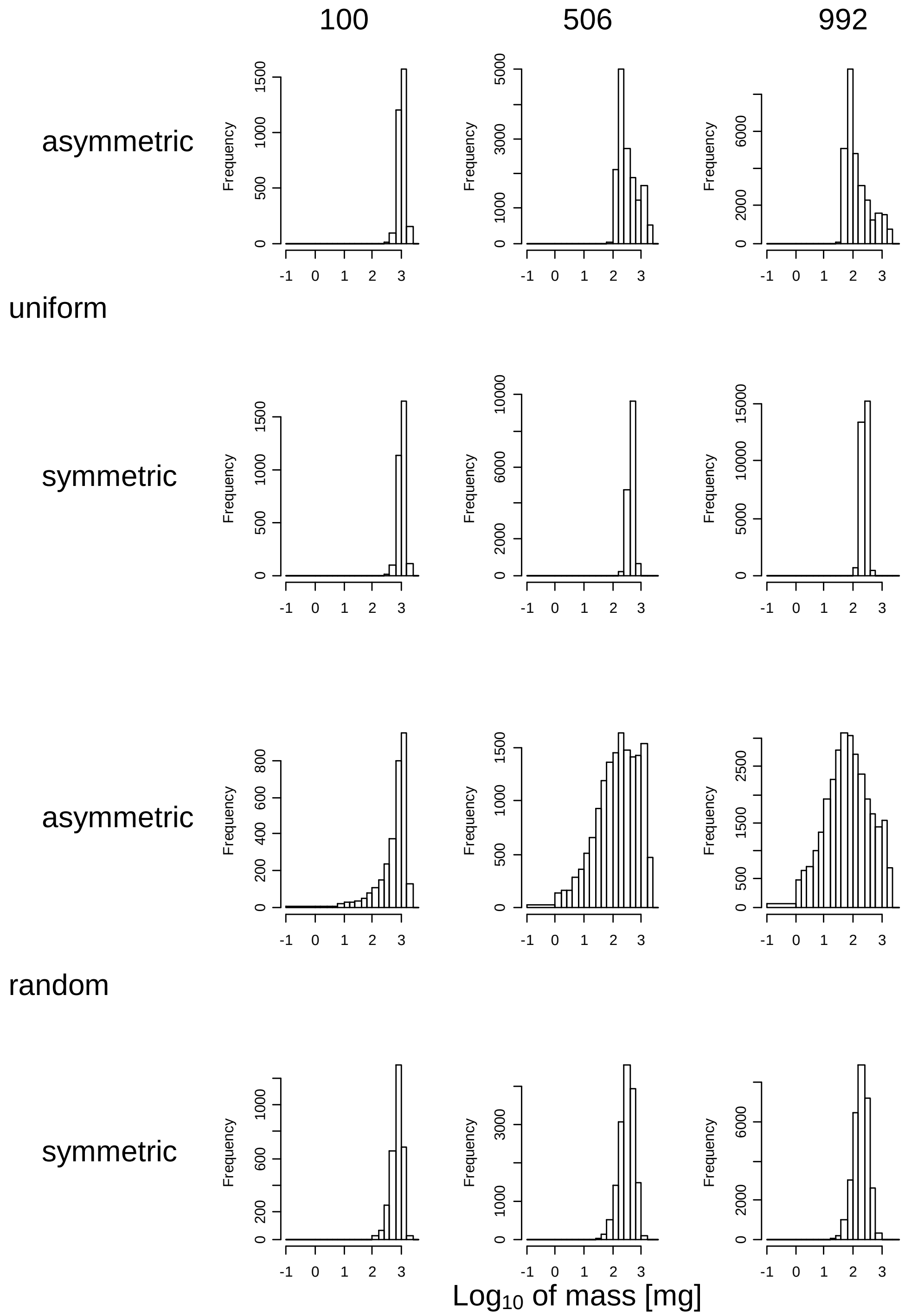

Figure 1. Histograms of biomass distributions of individual plants after 30 time steps with different simulation settings (results are out of all individual sizes of 30 replicates with identical settings, thus the high frequency numbers); the columns of histograms correspond to different densities (100, 506 and 992 individuals in the simulation area); the rows presents different spatial configurations (random or uniform (hexagonal packing) distributions) and different competition regimes (asymmetric or symmetric).

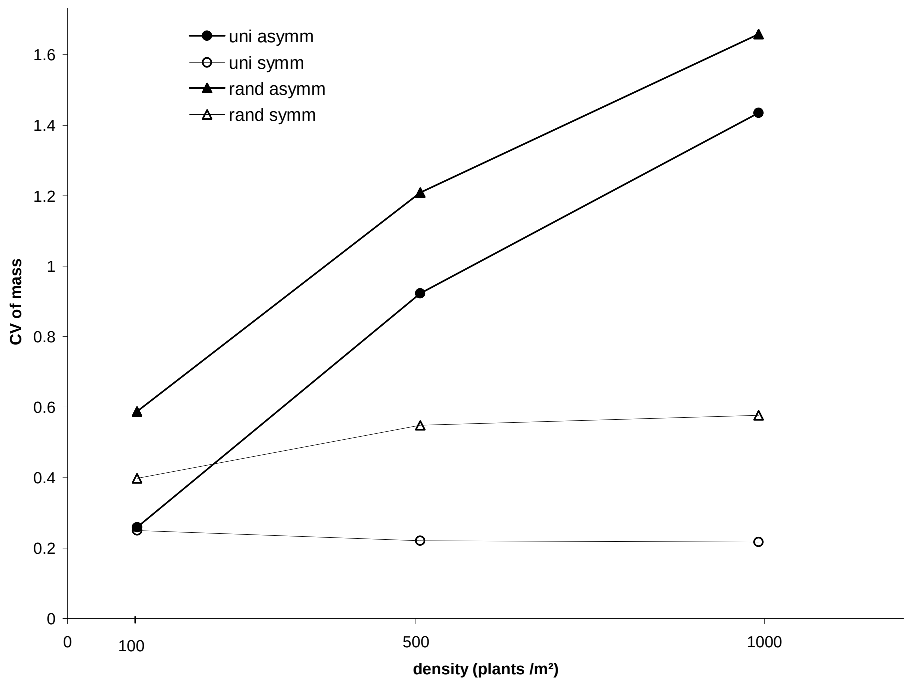

Figure 2. Coefficient of variation of mass versus density at time = 30 for different competition regimes (symmetric = white signs, asymmetric = black signs) and spatial configurations (random organization = triangles, hexagonal packing = circles).

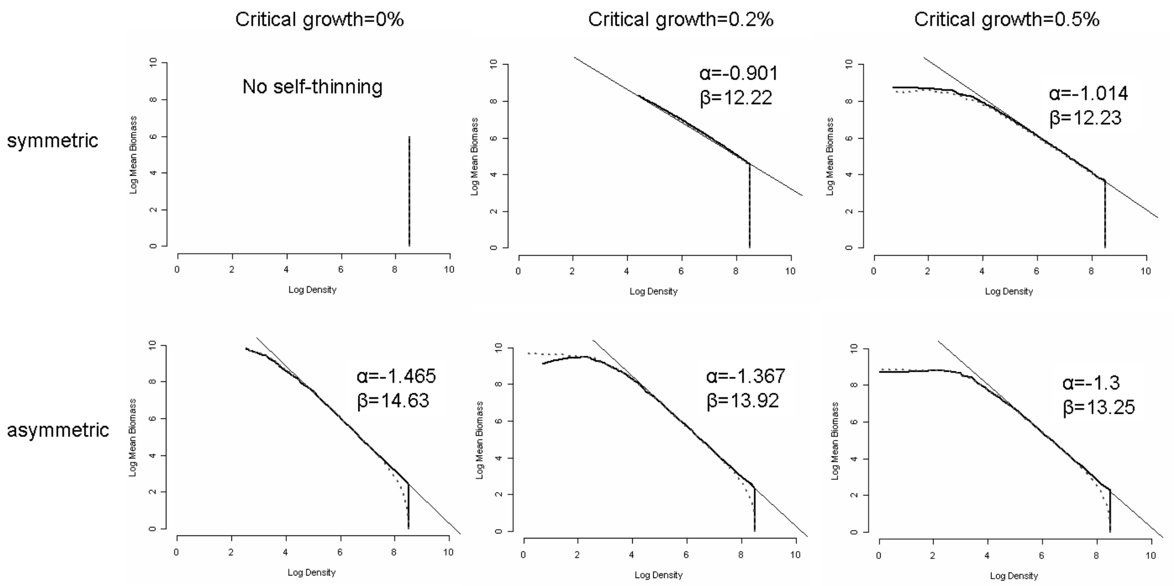

Figure 3. Results of the additional experiment looking at self-thinning trajectories depending on competition symmetry, installation of individuals and critical growth threshold. Black lines represent uniform initial installation, grey dashed lines represent random initial installation and thin lines are fitted regression lines on the linear part of the Log Density –Log Biomass relationship. α values represent the self-thinning trajectory (slope of the regression lines) and β values represent the intercept of the same regression model.

Tables

Table 1

Parameter	Description	Input value [unit]
Density	Number of plants to install on the simulation area	100; 506; 992 or 4970
Bmax-mean	Mean of maximal biomasses	20000 [mg]
Bmax-sd	Standard deviation of maximal biomasses	2000 [mg]
Bo-mean	Mean of initial biomasses	1.0 [mg]
Bo-sd	Standard deviation of initial biomasses	0.1 [mg]
r-mean	Mean of optimal growth rates	1 [$mg.cm^{-2}.time\ step^{-1}$]
r-sd	Standard deviation of optimal growth rates	0.1 [$mg.cm^{-2}.time\ step^{-1}$]