Model description

Florian D. Schneider

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We implement the equations for plant mortality and growth outlined above in a pair-approximation model of a spatially-explicit cellular automata framework. We contrast this to a model that does not account for spatial structure and assumes that the local neighborhood cover of plants is equal to the global vegetation cover, i.e. a mean field model.

Subsequently, we describe a basic form of the model that has been used by Noy-Meir and substitute it's elements with specific models of local plant-plant interactions. A system of ordinary differential equations is implemented in the framework of a mean-field approximation as well as a pair-approximation of a stochastic cellular automata model. We provide code for the mean-field approximation, the pair-approximation and the cellular automata online at https://cascade-wp6.github.com/livestock.

basic model

The framework provided by Noy-Meir is a graphical assessment of the attractors of the population dynamics in a simple predator-prey system. It describes mortality and growth as functions of global vegetation cover, ρ_1.

For vegetation mortality, M, we assume intrinsic plant mortality, i.e. the inverse of average lifespan, and add the mortality due to grazing risk as a classic type II functional response.

$$M(\rho_1) = m\rho_1 + \frac{a\rho_1 L}{1 + ah\rho_1} \,,$$

where m denotes the intrinsic mortality rate, a and h are the search efficiency and handling time of the nonlinear functional response (saturating at $1/h$) which is multiplied with the livestock density, L. Note that livestock density is defined in the unit number of grazers per area $\left[\frac{ind.}{ha}\right]$. Search efficiency a is given in area browsed in per time and grazer individual $\left[\frac{ha}{y \times ind.}\right]$, and handling time h is given in time per area consumed $\left[\frac{y}{ha}\right]$, which alltogether defines feeding rate as an area consumed per year by a single individual $\left[\frac{ha}{y \times ind.}\right]$. The overall change

of cover, $M(\rho)$, is thus independent from the size and unit of the observed area $[\frac{1}{y}]$.

The vegetation growth, G, is defined as a logistic growth function.

$$G(\rho_1) = r\rho_1(1 - \frac{\rho_1}{K})\,,$$

where the intrinsic growth rate, r, is neutralized when cover approaches the global carrying capacity, K. This reflects the global competition of plants fo resources of homoegeneous distribution, such as space: when all habitable space is occupied, plant growth falls to zero.

local feedbacks

The basic model assumes mortality and growth to be of homogeneous distribution, and neglects spatially-explicit effects. Here, we add plant-plant interactions at the local scale by taking the cover, q, in the direct vicinity of plants into account. By adding such interactions at the local level into the functions of growth and mortality, patterns emerge that act as positive or negative feedbacks on vegetation cover.

For vegetation growth, we assume that the local environmental suitability is enhanced by local facilitation (Milchunas et al 1998, Kéfi et al 2007). The reduction in growth rate, r, by aridity, i.e. the inverse of environmental quality b, is compensated by a function of $q_{0|1}$, the local density of cells in state 1 (i.e. vegetation) given that the focal cell is in state 0 (i.e. empty), and maximizes to one if the cell has four neighbors.

$$b = b^* + (1 - b^*)f q_{0|1}\,,$$

with the effect of aridity in absence of local vegetation being increased to the value of f if additive facilitation due to the presence of neighboring plants occurs. This term gradually determines the enhancement of the growth with an increasing local vegetation cover (maximizing at $q_{0|1} = 1$ if the cell has 4 neighbors).

As an opposing effect, we assume that local competition of plants inhibits colonisation locally by depleting nutrients or light. As cover increases and the interspace areas are closing in, the space available for rejuvenation approaches

zero. This is assuming that growth is diminished locally by competition, c. This affects carrying capacity rather than growth rate itself.

$$K = K^*(1 - cq_{0|1})$$

That is, if a cell has a fully vegetated local neighborhood, it's carrying capacity will be reduced by value c ($c \geq K$).

Regarding plant mortality, we implement two interactions into the model. In sparse environments, high local cover will be attracting grazers and concentrate plant mortality at locations with high local density. We assume that low plant cover reduces search efficiency, a, locally by the value v

$$a = a^* + v\frac{q_{1|1}}{\rho_1}$$

Thus, at low local cover feeding will be high on plants with neighbors, whereas at high cover the term has no effect since handling time is limiting consumption. An enhanced search efficiency will raise the critical thresholds for a collapse.

Opposing to that mechanism, plants in grazed habitats develop protective traits, such as thorns or cushion growth. They thereby provide protected habitat to their direct neighborhood, or share the investments in those traits with their neighbors. Overall grazing mortality thus is reduced through a decrease in local livestock densities by associational resistance, p.

$$L = L^*(1 - pq_{1|1})$$

Since $q_{1|1}$ and $q_{1|0}$ are spatially explicit expressions, these equations are referring to the situation at a particular location in space which is currently in one state or the other. The substitution into $M(\rho)$ and $G(\rho)$ yields transition probabilities, i.e. the probability for death and colonization for the given location, based on the global vegetation cover ρ_1 and the local vegetation cover $q_{1|1}$ or $q_{1|0}$ for vegetated or empty locations, respectively:

$$M(\rho_1, q_{1|1}) = w_{1,0} = m + \frac{(a^* + v\frac{q_{1|1}}{\rho_1})(1 - pq_{1|1})L\rho_1}{1 + (a^* + v\frac{q_{1|1}}{\rho_1})(1 - pq_{1|1})h\rho_1}$$

$$G(\rho_1, q_{1|0}) = w_{0,1} = \frac{r\rho_1(b^* + (1 - b^*)fq_{0|1})(1 - \frac{\rho_1}{K^*(1 - cq_{0|1})})}{1 - \rho_1}$$

Default parameters for the model are provided in table 1.

parameter	default value	unit	definition
r	1.0	$\left[\frac{1}{y}\right]$	max. reproduction rate of vegetation per year
b	0.5	unitless	environmental quality, a factor that indicates quality of enviro
K	0.9	unitless	carrying capacity of the system, a landscape specific valu
f	0	unitless	local facilitation, positive effect of plants on the colonizatio
c	0	unitless	local competition, negative effect of plants on colonization
m	0.05	$\left[\frac{1}{y}\right]$	intrinsic mortality of plants (inverse of av. lifespan)
v	0	unitless	attractant-decoy effect, negative effect of plants on m
p	0	unitless	associational resistance, positive protection effects of plants o
L	2	$\left[\frac{ind.}{ha}\right]$	Livestock density
h	20	$\left[\frac{y}{ha}\right]$	handling time, time required to consume one hectar
a	10	$\left[\frac{ha}{y \times ind.}\right]$	search efficiency of livestock,

pair-approximation model

Subsequently, we implement these functions into a pair-approximation of a spatially-explicit model. The pair-approximation framework (Matsuda et al. 1992) is defined as a system of ordinary differential equations, describing the populations of *pairs* of neighboring locations. By this book-keeping, we also keep track of the average local cover in the neighborhood of vegetated ($q_{1,1}$) and unvegetated ($q_{0,1}$) locations in the landscape. In a two state system, three pairs can be defined with population densities $\rho_{1,1}$, $\rho_{0,0}$, and $\rho_{0,1}$. Besides, there are the population densities of the singletons, ρ_0 and ρ_1.

The following conservation equations allow to calculate population densities of one pair based on the other pairs and singletons:

$$\rho_1 + \rho_0 = 1$$

$$\rho_{1,1} + \rho_{0,1} = \rho_1$$

$$\rho_{0,1} + \rho_{0,0} = \rho_0$$

We now can use the transition probabilities of the individual locations to describe the full system of differential equations.

$$\frac{\mathrm{d}\rho_1}{\mathrm{d}t} = \rho_0 w_{0,1} - \rho_1 w_{1,0}$$

$$\frac{\mathrm{d}\rho_{1,1}}{\mathrm{d}t} = 2\rho_{1,0}w_{0,1} - 2\rho_{1,1}w_{1,0}$$

$$\frac{\mathrm{d}\rho_{1,0}}{\mathrm{d}t} = 2\rho_{0,0}w_{0,1} + 2\rho_{1,1}w_{1,0} - \rho_{1,0}w_{0,1}$$

$$\frac{\mathrm{d}\rho_{0,0}}{\mathrm{d}t} = 2\rho_{1,0}w_{1,0} - 2\rho_{0,0}w_{0,1}$$

$$\frac{\mathrm{d}\rho_0}{\mathrm{d}t} = \rho_1 w_{1,0} - \rho_0 w_{0,1}$$

Due to the conservation equations, two of these are sufficient to fully describe the dynamics of the system. We chose to keep the first two representing the density of vegetated cells ρ_1 and the density of pairs of vegetated cells $\rho_{1,1}$ and subsitute therein $\rho_0 = 1 - \rho_1$ and $\rho_{1,0} = \rho_1 - \rho_{1,1}$:

$$\frac{\mathrm{d}\rho_1}{\mathrm{d}t} = (1 - \rho_1)w_{0,1} - \rho_1 w_{1,0}$$

$$\frac{\mathrm{d}\rho_{1,1}}{\mathrm{d}t} = 2(\rho_1 - \rho_{1,1})w_{0,1} - 2\rho_{1,1}w_{1,0}$$

These two equations are implemented in the package as function `lifestock$pairs()`, which is then called by the ODE-solver. The object `rho` is a list object that contains global cover at first position and global cover of pair (1,1) at second position.

```
delta_1 = (1-rho[[1]]) * colonization(rho, parms) -
                rho[[1]] * death(rho, parms)
delta_11 = 2 * (rho[[1]]-rho[[2]]) * colonization(rho, parms) -
                2 * rho[[2]] * death(rho, parms)
```

The functions `colonization()` and `death()` are defined in `R/definitions.R`

To substitute the transition probabilities $M(\rho_1, q_{1|1}) = w_{1,0}$ and $G(\rho_1, q_{1|0}) = w_{0,1}$ in these equtions, we require definitions of local cover in the terms of the

pair-approximation framework. Since formally $q_{i|j}$ is a conditional probability (given that one neighbor is in state i, what is the probability to find the other in state j) we can express it in terms of densities of pairs and 'singletons,' as

$$q_{i|j} = \frac{\rho_{ij}}{\rho_i}$$

thus,

$$q_{0|1} = \frac{\rho_{10}}{\rho_0} = \frac{\rho_1 - \rho_{11}}{1 - \rho_1}$$

$$q_{1|1} = \frac{\rho_{11}}{\rho_1}$$

Now, substitution yields

$$\frac{\mathrm{d}\rho_{11}}{\mathrm{d}t} = 2(\rho_1 - \rho_{11}) \frac{r\rho_1^{1+\alpha}(b^* + (1-b)f\frac{\rho_1 - \rho_{11}}{1-\rho_1}))(1 - \frac{\rho_1}{K^*(1-c\frac{\rho_1 - \rho_{11}}{1-\rho_1})})}{1 - \rho_1} - 2\rho_{11}m - 2\rho_{11}\frac{(a^* + v\frac{\rho_{11}}{\rho_1})L^*(1 - p\frac{\rho_{11}}{\rho_1}}{1 + (a^* + v\frac{\rho_{11}}{\rho_1})h\rho_1^{1+}}$$

$$\frac{\mathrm{d}\rho_1}{\mathrm{d}t} = r\rho_1^{1+\alpha}(b^* + (1-b)f\frac{\rho_1 - \rho_{11}}{1-\rho_1})(1 - \frac{\rho_1}{K^*(1 - c\frac{\rho_1 - \rho_{11}}{1-\rho_1})}) - \rho_1 m - \frac{(a^* + v\frac{\rho_{11}}{\rho_1})L^*(1 - p\frac{\rho_{11}}{\rho_1})\rho_1^{1+q}}{1 + (a^* + v\frac{\rho_{11}}{\rho_1})h\rho_1^{1+q}}$$

References

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