1 The Model Formulation

Here we briefly describe the mathematical formulation used in the `stagePop` however for full details the reader should consult ([1, 3, 2]).

For any stage-structured species, if the number of individuals in stage i is given by N_i, then based on simple book-keeping:

$$\dot{N}_i(t) = R_i(t) - M_i(t) - D_i(t)N_i(t) \tag{1}$$

where R_i is the rate of recruitment into class i, M_i is the rate of maturation out of class i and D_i is the per capita death rate of organisms in stage i. The rate of maturation, M_i, from stage i at time t is given by

$$M_i(t) = R_i(t - \tau_i(t))P_i(t)[1 - \dot{\tau}_i(t)] \tag{2}$$

where $P_i(t)$ is the fraction of individuals entering stage i at $t - \tau_i(t)$ that has survived to time t. Assuming individuals are born into stage 1, the reproductive stage is r, β is the reproductive function and I is the immigration rate, then recruitment into the first stage is given by

$$R_1(t) = \beta(N_r(t)) + I_1(t). \tag{3}$$

and, into subsequent stages by

$$R_{i+1}(t) = M_i(t) + I_{i+1}(t), \text{ for } i = 1, ..., r. \tag{4}$$

Note that immigrants are assumed to be 'new born' into whichever stage they enter (i.e. with respect to age or size etc they are at the beginning of their entry stage).

The fraction of individuals which enter stage i at $t - \tau_i$ and survive to time t is given by

$$P_i(t) = \exp\left(\int_{t-\tau_i(t)}^{t} -D_i(x)dx\right). \tag{5}$$

However in order to avoid solving integro-differential equations, P_i is replaced by its time derivative,

$$\dot{P}_i(t) = P_i(t)[D_i(t - \tau_i(t))[1 - \dot{\tau}_i(t)] - D_i(t)], \tag{6}$$

plus an initial condition, $P_i(0) = \exp(-D_i(0)\tau_i(0))$. The rate of change of the stage duration, $\dot{\tau}_i$, is defined in terms of $g_i(t)$ which is the rate at which an individual develops within stage i at any given time, t. If $g(t)$ is considered to be the rate of change of a development index (e.g. size, age, nutrient levels etc) that goes from 0 at the start of the stage to γ at the end, then $\tau_i(t)$ is determined by the requirement

$$\int_{t-\tau_i(t)}^{t} g_i(x)dx = \gamma. \tag{7}$$

Differentiating this gives,

$$g(t) - g(t - \tau(t))\frac{d}{dt}(t - \tau(t)) = 0, \tag{8}$$

and thus the rate of change of τ is given by

$$\dot{\tau}_i(t) = 1 - \frac{g_i(t)}{g_i(t - \tau_i(t))}. \tag{9}$$

For a more detailed explanation, consult Section 8.5 in [2].

If the functions (or parameters) D_i, g_i (or τ_i if τ_i is time independent) and β are defined, and the initial histories (i.e for $-\tau_i \leq t \leq 0$) for N_i, τ_i and P_i are provided, Equations 1-9 completely define the population dynamics of any stage-structured species.

1.1 Assumptions

In `stagePop` we make the following assumptions for the initial histories:

$$\begin{aligned}
R_i(t) &= 0 \text{ for all } t \leq 0, && (10)\\
I_i(t) &= 0 \text{ for all } t \leq 0, && (11)\\
N_i(t) &= N_i(0) \text{ for all } t \leq 0, && (12)\\
D_i(t, N_i(t)) &= D_i(0, N_i(0)) \text{ for all } t \leq 0 \text{ if } D = D(t), && (13)\\
g_i(t, N_i(t)) &= g_i(0, N_i(0)) \text{ for all } t \leq 0 \text{ if } \tau = \tau(t). && (14)
\end{aligned}$$

1.2 Multiple Species

For predator-prey, host-parasitoid and consumer-resource systems there can be multiple interacting species (bearing in mind here we can consider food as a 'species'). In this case each species is essentially modelled separately but the species may interact in the functions for death rates, reproductive rates and developmental rates.

1.3 Simplifications

If the stage duration, τ_i, does not change with time (i.e. when "`timeDependDuration`" is '`FALSE`' in the call to **popModel()**, as in the blowflies, larval competition, predator-prey and host-parasitoid examples), then Equations 2, 6 and 9 reduce to

$$\begin{aligned}
M_i(t) &= R_i(t - \tau_i)P_i(t) && (15)\\
\dot{P}_i(t) &= P_i(t)(D_i(t - \tau_i) - D_i(t)) && (16)\\
\dot{\tau}_i(t) &= 0. && (17)
\end{aligned}$$

Furthermore, if D_i also does not change with time (i.e. when "`timeDependDeath`" is '`FALSE`' in the call to **popModel()** as in the blowflies example), then Equations 5 and 6 reduce to

$$\begin{aligned}
P_i(t) &= \exp(-D_i\tau_i) && (18)\\
\dot{P}_i(t) &= 0. && (19)
\end{aligned}$$

References

[1] Gurney WSC, RM Nisbet and JH Lawton. 1983. The systematic formulation of tractable single-speices population models incorporating age structure. Journal of Animal Ecology. 52 (2), 479-495.

[2] Gurney WSC and RM Nisbet. 1998. Ecological Dynamics.

[3] Nisbet RM and WSC Gurney. 1983. The systematic formulation of population models for insects with dynamically varying instar duration. Theoretical Population Biology, 23, 114-135.