

Supporting Information S1 - Model formulations and derivations

Supporting Information for *How do MAR(1) models cope with hidden nonlinearities in ecological dynamics?*

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1 The connection between MAR(1) models and Gompertz population dynamics

The multispecies Gompertz dynamics with S interacting species is formulated as:

$$n_{i,t+1} = n_{i,t} + r_i - \sum_{j=1}^S \alpha_{ij} n_{j,t} + w_{i,t} \quad (1)$$

Here, n_i is the ln-abundances of the i^{th} species, r_i its growth rate at zero ln-density, α_{ij} represents competition between the i^{th} and j^{th} species and $w_{i,t}$ corresponds to Gaussian random process error on the per capita growth rate (i.e., mimicking classic environmental stochasticity in birth and death rates without autocorrelation). In this paper, species variables with uppercase letters will refer to abundances, while lowercase letters will refer to natural ln-abundances, i.e., $n = \ln(N)$. In simplified matrix form, multispecies Gompertz dynamics writes:

$$\mathbf{n}_{t+1} = \mathbf{r} - (\mathbf{I} - \mathbf{A})\mathbf{n}_t + \mathbf{w}_t, \mathbf{w}_t \sim \text{MVN}(0, \Sigma) \quad (2)$$

in which the i^{th} and j^{th} elements of the matrix \mathbf{A} are α_{ij} , and \mathbf{I} is the identity matrix. Suppose that some of the species are affected by environmental variables \mathbf{u}_t . This is often modelled as a linear effect on growth rates using a coefficient matrix \mathbf{Q} :

$$\mathbf{r}_t = \mathbf{r} + \mathbf{Q}\mathbf{u}_t \quad (3)$$

Combining eq. 2 and 3 leads to the MAR(1) master equation of Ives *et al.* (2003) and Hampton *et al.* (2013):

$$\mathbf{x}_{t+1} = \mathbf{a} + \mathbf{B}\mathbf{x}_t + \mathbf{C}\mathbf{u}_t + \mathbf{w}_t, \mathbf{w}_t \sim \text{MVN}(0, \Sigma) \quad (4)$$

in which \mathbf{x} is the vector of species ln-abundance, the intercept \mathbf{a} corresponds to the zero ln-density growth rate \mathbf{r} , $\mathbf{B}=\mathbf{I}-\mathbf{A}$ relates to the competition coefficients \mathbf{A} , and \mathbf{C} corresponds to the environmental effects \mathbf{Q} on species growth rates. Therefore, in a competition context, fitted \mathbf{B} coefficients derived from ln-transformed abundances could be interpreted as the mechanistic coefficients of a Gompertz model. In the general case (e.g., food webs, multitype networks, other types of competitive systems), however, assuming Gompertz density-dependence has no such mechanistic connection. It might be worth noting that the MAR(1) model is a vector version of the AR(1) model, which is itself a discrete-time version of the Ornstein-Uhlenbeck process, which, in turn, is a mean-reverting random walk for the right parameterization.

2 MAR(1) model as a first order approximation of unknown dynamics

The applicability of MAR(1) models is not restricted to Gompertz dynamics, for Ives *et al.* (2003) showed a mapping between \mathbf{B} and the Jacobian matrix \mathbf{J} for a general nonlinear model. If species ln-abundance \mathbf{n}_{t+1} is a non-linear, stochastic function of ln-abundances \mathbf{n}_t and environmental covariates \mathbf{u}_t such that $\mathbf{n}_{t+1} = f(\mathbf{n}_t, \mathbf{u}_t)$, which is stationary around equilibrium \mathbf{n}^* , the linear approximation of this process around the equilibrium ln-abundances \mathbf{n}^* and for environmental variables standardized with mean $\mathbf{0}$ is:

$$f(\mathbf{n}_t, \mathbf{u}_t) \approx f(\mathbf{n}^*, \mathbf{0}) + \frac{\partial f}{\partial \mathbf{n}}(\mathbf{n}^*, \mathbf{0})[\mathbf{n}_t - \mathbf{n}^*] + \frac{\partial f}{\partial \mathbf{u}}(\mathbf{n}^*, \mathbf{0})[\mathbf{u}_t - \mathbf{0}] \quad (5)$$

The matrix of partial derivatives with respect to species ln-abundances is the Jacobian matrix \mathbf{J} and predicts the dynamics of the system near equilibrium. The matrix of partial derivatives with respect to environment simplifies to \mathbf{Q} when the environmental effect is as described by eq. 3. Therefore, setting $\mathbf{x}_t = \mathbf{n}_t - \mathbf{n}^*$ leads to:

$$\mathbf{x}_{t+1} \approx \mathbf{J}\mathbf{x}_t + \mathbf{Q}\mathbf{u}_t \quad (6)$$

which clearly shows how \mathbf{B} corresponds to \mathbf{J} , \mathbf{C} corresponds to \mathbf{Q} and the intercept vector \mathbf{a} is a zero vector. Note that such mapping applies to ln-transformed centered abundances, in which case the MAR(1) model must be fitted without intercept.

3 Formal description of the data-generating models for our simulation experiment

3.1 GOMPERTZ COMPETITION

The first data-generating model we introduce is the discrete-time Gompertz model (e.g., Mutshinda *et al.*, 2009), which will serve as a control as its mechanistic parameters map perfectly with the MAR(1) model (which differs only in terms of parameterization and interpretation). In untransformed scale, the Gompertz two-species competition model can be written

$$N_{1,t+1} = N_{1,t}e^{r_1}N_{1,t}^{-\alpha_{11}}N_{2,t}^{-\alpha_{12}} \quad (7)$$

$$N_{2,t+1} = N_{2,t}e^{r_2}N_{1,t}^{-\alpha_{21}}N_{2,t}^{-\alpha_{22}} \quad (8)$$

The equations for the ln-abundance then write:

$$n_{1,t+1} = n_{1,t} + r_1 - \alpha_{11}n_{1,t} - \alpha_{12}n_{2,t} \quad (9)$$

$$n_{2,t+1} = n_{2,t} + r_2 - \alpha_{21}n_{1,t} - \alpha_{22}n_{2,t} \quad (10)$$

Where r_i stands for the intrinsic growth rate, α_{ij} for intra- and inter-specific effects of species j on species i . The equilibrium ln-abundances for the two species are $n_1^* = \frac{\alpha_{12}r_2 - r_1\alpha_{22}}{\alpha_{21}\beta_{12} - \alpha_{11}\alpha_{22}}$ and $n_2^* = \frac{\alpha_{21}r_1 - r_2\alpha_{11}}{\alpha_{21}\alpha_{12} - \alpha_{11}\alpha_{22}}$. The first order Taylor expansion around the equilibrium point leads to the following Jacobian matrix:

$$\mathbf{J} = \begin{pmatrix} 1 - \alpha_{11} & -\alpha_{12} \\ -\alpha_{21} & 1 - \alpha_{22} \end{pmatrix} \quad (11)$$

By fitting a MAR(1) model to centered data generated by such model, the fitted elements of the \mathbf{B} matrix correspond to the elements of \mathbf{J} . Because all jacobian elements relate directly to a single parameter of the Gompertz model, the fitted \mathbf{B} matrix elements can directly be interpreted ecologically in terms of intra and inter-specific competition strength.

3.2 RICKER COMPETITION

The Ricker model is well known to fisheries ecologist for introducing density-dependent effects in recruitment (Ricker, 1954), and is known to produce overcompensation as the intrinsic growth rates r increases above 1 (similarly to the logistic map, Kot, 2001). We extend this model to a two-species competition model (eqs. 12,13 below) in which both species present density-dependent regulation of type Ricker. Such model has been used extensively to mimic Lotka-Volterra competition in discrete time (Ives 1995; Ives *et al.* 2008). It differs nonetheless from the continuous time version, and the Beverton-Holt dynamics (see below), by its ability to promote cycles and chaos for high growth rates, like the single-species version.

$$N_{1,t+1} = N_{1,t} \exp(r_1 - \alpha_{11}N_{1,t} - \alpha_{12}N_{2,t}) \quad (12)$$

$$N_{2,t+1} = N_{2,t} \exp(r_2 - \alpha_{21}N_{1,t} - \alpha_{22}N_{2,t}) \quad (13)$$

The discrete-time equations for the ln-abundance of two competing species following with Ricker density-dependence writes:

$$n_{1,t+1} = n_{1,t} + r_1 - \alpha_{11}e^{n_{1,t}} - \alpha_{12}e^{n_{2,t}} \quad (14)$$

$$n_{2,t+1} = n_{2,t} + r_2 - \alpha_{22}e^{n_{2,t}} - \alpha_{21}e^{n_{1,t}} \quad (15)$$

This formulation leads to the following equilibriums $n_1^* = \ln\left(\frac{\alpha_{12}r_2 - r_1\alpha_{22}}{\alpha_{21}\alpha_{12} - \alpha_{11}\alpha_{22}}\right)$ and $n_2^* = \ln\left(\frac{\alpha_{21}r_1 - r_2\alpha_{11}}{\alpha_{21}\alpha_{12} - \alpha_{11}\alpha_{22}}\right)$ and the Jacobian matrix evaluated in the neighbourhood of the equilibrium becomes:

$$\mathbf{J} = \begin{pmatrix} 1 - \alpha_{11}e^{n_1^*} & -\alpha_{12}e^{n_2^*} \\ -\alpha_{21}e^{n_1^*} & 1 - \alpha_{22}e^{n_2^*} \end{pmatrix} \quad (16)$$

Now, because equilibrium values enter the Jacobian, the fitted parameters of the \mathbf{B} matrix actually correspond to a mixture of mechanistic parameters of the underlying dynamics. With a data-generating model of the Ricker type, the elements of the fitted \mathbf{B} matrix do not correspond to ecological processes per se, but rather to a mix of ecological processes. This is why fitted \mathbf{B} matrices are often said to be “phenomenological”: their elements describe the “net effect” of one species on another when the model is linearly approximated around its equilibrium, but that net effect might well result from a mixture of ecological processes that cannot be disentangled easily. This is also why the ecological interpretation of the fitted \mathbf{B} matrix can be challenging when a MAR(1) model is used as an approximation of another, unknown non-linear model.

3.3 BEVERTON-HOLT COMPETITION

The last of our data-generating competition models is the Beverton-Holt model, after the equations initially developed in fisheries science by Beverton & Holt (Beverton & Holt, 1957). This model, more stable than its Ricker counterpart (Kot, 2001), is described in eqs. 17,18 and eqs. 19,20 in natural logarithmic scale.

$$N_{1,t+1} = \frac{e^{r_1}N_{1,t}}{1 + \alpha_{11}N_{1,t} + \alpha_{12}N_{2,t}} \quad (17)$$

$$N_{2,t+1} = \frac{e^{r_2}N_{2,t}}{1 + \alpha_{21}N_{1,t} + \alpha_{22}N_{2,t}} \quad (18)$$

$$n_{1,t+1} = r_1 + n_{1,t} - \ln(1 + \alpha_{11}N_{1,t} + \alpha_{12}N_{2,t}) \quad (19)$$

$$n_{2,t+1} = r_2 + n_{2,t} - \ln(1 + \alpha_{21}N_{1,t} + \alpha_{22}N_{2,t}) \quad (20)$$

and leads to similar equilibrium values as the Ricker model. The corresponding Jacobian matrix has a rather different form:

$$\mathbf{J} = \begin{pmatrix} 1 - \frac{\alpha_{11}e^{n_1^*}}{1 + \alpha_{11}e^{n_1^*} - \alpha_{12}e^{n_2^*}} & -\frac{-\alpha_{12}e^{n_2^*}}{1 + \alpha_{11}e^{n_1^*} - \alpha_{12}e^{n_2^*}} \\ -\frac{-\alpha_{21}e^{n_1^*}}{1 + \alpha_{22}e^{n_2^*} - \alpha_{21}e^{n_1^*}} & 1 - \frac{\alpha_{22}e^{n_2^*}}{1 + \alpha_{22}e^{n_2^*} - \alpha_{21}e^{n_1^*}} \end{pmatrix} \quad (21)$$

This suggests that direct interpretation of the fitted \mathbf{B} matrix coefficients in term of mechanistic parameters might be even more challenging under the Beverton-Holt framework than with the Ricker model. We do note, however, that equations (19, 20) are closer to Gompertz than Ricker density-dependence because the effect of summed densities on the growth rate is ln-transformed.

3.4 PREDATOR-PREY DYNAMICS: LOTKA-VOLTERRA INTERACTION WITH RICKER DENSITY-DEPENDENCE (LVR)

We now extend our set of data generating models by including asymmetrical model structures in discrete time representing prey-predator dynamics. We start with a model where prey density N has Ricker density-dependence and the predator P consumes the prey and dies at fixed rates, in a Lotka-Volterra-like setup (eqs. 22,23). We will thereafter refer to this model using the ‘‘LVR’’ acronym. In ln-abundances, this model is described by eqs 24,25

$$N_{t+1} = N_t \exp(r - \alpha N_t - \gamma P_t) \quad (22)$$

$$P_{t+1} = P_t \exp(\varepsilon \gamma N_t - \mu) \quad (23)$$

$$n_{t+1} = n_t + r - \alpha e^{n_t} - \gamma e^{p_t} \quad (24)$$

$$p_{t+1} = p_t + \varepsilon \gamma e^{n_t} - \mu \quad (25)$$

Here, in addition to the intrinsic growth rate r and intra-specific competition α , we introduce parameter γ that represents the predator attack rate, ε the predator assimilation rate and μ the predator death rate. Note that since the predator has no intrinsic growth rate as its population growth depends on food intake, we introduced stochasticity within the death rate instead (the process noise is still additive on a ln-scale).

Prey and predator’s equilibrium abundances on a ln-scale are then $n^* = \ln\left(\frac{\mu}{\varepsilon\gamma}\right)$ and $p^* = \ln\left(\frac{r}{\gamma} - \frac{\alpha\mu}{\varepsilon\gamma^2}\right)$, and the Jacobian matrix evaluated around equilibrium is

$$\mathbf{J} = \begin{pmatrix} 1 - \frac{\alpha\mu}{\varepsilon\gamma} & -r + \frac{\alpha\mu}{\varepsilon\gamma} \\ \mu & 1 \end{pmatrix} \quad (26)$$

Here as well, for a non-linear predator-prey system (due to Ricker density-dependence), the elements of the fitted \mathbf{B} matrix correspond to a mixture of ecological processes. The upper-left corner element in eq. (26) for example, which could in a MAR(1) model be interpreted as ‘‘prey density dependence’’ does not only depend on prey intra-specific competition α , but also on predator mortality μ , predator attack rate γ and predator assimilation rate ε . Note that even though intrinsic growth rate r is absent from j_{11} , we still expect a relationship between r and j_{11} due to the feasibility conditions on the predator equilibrium density (which needs to be positive). This indirect relationship between r and j_{11} explains why $j_{11} < 0$ still indicate overcompensation in the LVR model. Note also that in this model, the predator is only regulated by the prey and not by itself, which leads to the lower-right

element of the Jacobian to take the constant value of 1. Furthermore, the prey growth rate does not affects its equilibrium abundance and therefore, the PRESS perturbation only affects the predator equilibrium abundance. This also holds for the prey-predator system with type II functional response (below).

3.5 PREDATOR-PREY DYNAMICS WITH A TYPE II FUNCTIONAL RESPONSE (LVR-T2):

The LVR-T2 model is akin to the Rosenzweig-MacArthur model, but its discrete nature allows for a larger range of dynamical behaviors, including chaos. Similar equations to eqs. (27,28) have been employed by Ives and coauthors (Ives, 1995; Ives *et al.*, 1999). In a natural logarithmic scale, the model is given by eqs. (29,30).

$$N_{t+1} = N_t \exp\left(r - \alpha N_t - \frac{\gamma}{1 + hN_t} P_t\right) \quad (27)$$

$$P_{t+1} = P_t \exp\left(\varepsilon \frac{\gamma}{1 + hN_t} N_t - \mu\right) \quad (28)$$

$$n_{t+1} = n_t + r - \alpha e^{n_t} - \frac{\gamma}{1 + \gamma h e^{n_t}} e^{p_t} \quad (29)$$

$$p_{t+1} = p_t + \frac{\varepsilon \gamma}{1 + \gamma h e^{n_t}} e^{n_t} - \mu \quad (30)$$

The only additional parameter to eqs (22,23) is the handling time h of the prey by the predator. Due to the non-linearity induced by the type II functional response, equilibrium values are now $n^* = \ln\left(\frac{\mu}{\gamma(\varepsilon - \mu h)}\right)$ and $p^* = \ln\left(\frac{\varepsilon^2 r - \varepsilon \mu (h + \alpha \gamma^{-1})}{\gamma(\varepsilon - \mu h)^2}\right)$ and the Jacobian becomes a little more intricate:

$$\mathbf{J} = \begin{pmatrix} 1 - \alpha e^{n^*} + \frac{\gamma^2 h e^{n^*} e^{p^*}}{(\gamma h e^{n^*} + 1)^2} & \frac{-\gamma e^{p^*}}{\gamma h e^{n^*} + 1} \\ \frac{\gamma \varepsilon e^{n^*}}{(\gamma h e^{n^*} + 1)^2} & 1 \end{pmatrix} \quad (31)$$

This model can either present a stable equilibrium (and possibly quasi-cycles around it when stochasticity is added) or it can display limit cycles. These two dynamical behaviours can be identified through the dominant norm of the Jacobian matrix that should be <1 in the case of stable equilibrium and >1 with limit cycles. To know how MAR(1) performs in both cases, we treat them as two separate data-generating models, termed LVR-T2-point and LVR-T2-cycle.

3.6 HOST-PARASITOID DYNAMICS FROM MAY-HASELL MODEL.

Our last data-generating model describes in eqs (32,33) the dynamic of a host H and its parasitoid P :

$$H_{t+1} = H_t \exp(r) A(P_t) \quad (32)$$

$$P_{t+1} = c H_t (1 - A(P_t)) \quad (33)$$

Its ln-transformed form writes:

$$h_{t+1} = h_t + r + \ln(A(P_t)) \quad (34)$$

$$p_{t+1} = \ln(c) + h_t + \ln(1 - A(P_t)) \quad (35)$$

Where r is the intrinsic growth rate of the host, c is the average number of female parasitoids sprouting from an host, and $A(P_t)$ is a function of parasitoid abundance that represents the average proportion of hosts escaping parasitism. The fraction $A(P_t)$ can take many forms, but for our purpose

we use $A(P_t) = \left(1 + \frac{bP_t}{l}\right)^{-l}$ where b stands for the searching efficiency of the parasitoid and l is an index defining the degree to which the distribution of parasitism amongst the host is aggregated (most aggregated with $l = 0$ or random when $l \rightarrow +\infty$). This functional form follows May (1978) and Hassell (2000). The model presents a stable equilibrium at the following host and parasitoid ln-abundances: $h^* = \ln\left(\frac{\frac{l}{b}(e^{r/l}-1)}{c(1-e^{-r})}\right)$ and $p^* = \frac{l}{b}(e^{r/l}-1)$. Hence, the Jacobian evaluated around this equilibrium writes:

$$\mathbf{J} = \begin{pmatrix} 1 & -be^{p^*} \left(1 + \frac{b}{l}e^{p^*}\right)^{(-2l-1)} \\ 1 & e^{p^*} \left(\frac{b\left(1 + \frac{b}{l}e^{p^*}\right)^{(-l-1)}}{1 - \left(1 + \frac{b}{l}e^{p^*}\right)^{-l}}\right) \end{pmatrix}$$

Here, it is interesting to note that all regulating mechanisms are provided by the parasitoid, not by the host, as the host has exponential growth without the parasitoid. This explains why the first column of the Jacobian matrix is filled with ones.

References

- Beverton, R.J.H. & Holt, S.J. (1957) On the dynamics of exploited fish populations. *Fishery Investigations Series II Volume XIX, Ministry of Agriculture, Fisheries and Food*.
- Hampton, S., Holmes, E., Scheef, L., Scheuerell, M., Katz, S., Pendleton, D. & Ward, E. (2013) Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. *Ecology*, **94**, 2663–2664.
- Hassell, M.P. (2000) Host-parasitoid population dynamics. *Journal of Animal Ecology*, **69**, 543–566.
- Ives, A., Dennis, B., Cottingham, K.L. & Carpenter, S.R. (2003) Estimating Community Stability and Ecological Interactions from time series data. *Ecological Monographs*, **73**, 301–330.
- Ives, A., Einarsson, A., Jansen, V. & Gardarsson, A. (2008) High-amplitude fluctuations and alternative dynamical states of midges in lake myvatn. *Nature*, **452**, 84–87.
- Ives, A.R., Gross, K. & Klug, J.L. (1999) Stability and variability in competitive communities. *Science*, **286**, 542–544.
- Ives, A.R. (1995) Predicting the Response of Populations to Environmental Change. *Ecology*, **76**, 926–941.
- Kot, M. (2001) *Elements of Mathematical Ecology*. Cambridge University Press.
- May, R. (1978) Host-parasitoid systems in patchy environments: a phenomenological model. *Journal of Animal Ecology*, **47**, 833–844.
- Mutshinda, C.M., O’Hara, R.B. & Woiwod, I.P. (2009) What drives community dynamics? *Proceedings Biological sciences / The Royal Society*, **276**, 2923–2929.
- Ricker, W. (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, **11**, 559–623.