

How do MAR(1) models cope with hidden nonlinearities in ecological dynamics?

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Abstract

1. Multivariate autoregressive (MAR) models are an increasingly popular technique to infer interaction strengths between species in a community and to predict the community response to environmental change. The most commonly employed MAR(1) models, with one time lag, can be viewed either as multispecies competition models with Gompertz density dependence or, more generally, as a linear approximation of more complex, nonlinear dynamics around stable equilibria. This latter interpretation allows for broader applicability, but may come at a cost in terms of interpretation of estimates and reliability of both short- and long-term predictions.
2. We investigate what these costs might be by fitting MAR(1) models to simulated 2-species competition, consumer-resource and host-parasitoid systems, as well as a larger food web influenced by the environment. We review how MAR(1) coefficients can be interpreted and evaluate how reliable are estimates of interaction strength, rank, or sign; accuracy of short-term forecasts; as well as the ability of MAR(1) models to predict the long-term responses of communities submitted to environmental change such as PRESS perturbations.
3. The net effects of species j on species i are usually (90%-95%) well recovered in terms of sign or rank, with the notable exception of overcompensatory dynamics. In actual values, net effects of species j on species i are not well recovered when the underlying dynamics are nonlinear. MAR(1) models are better at making short-term qualitative forecasts (next point going up or down) than at predicting long-term responses to environmental perturbations, which can be severely over- as well as underestimated.
4. We conclude that when applying MAR(1) models to ecological data, inferences on net effects among species should be limited to signs, or the Gompertz assumption should be tested and discussed. This particular assumption on density-dependence (log-linearity) is also required for unbiased long-term predictions. Overall, we think that MAR(1) models are highly useful tools to resolve and characterize community dynamics, but we recommend to use them in conjunction with alternative, nonlinear models resembling the ecological context in order to improve their interpretation in specific applications.

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KEYWORDS

forecasting, interaction strength, MARSS, multivariate autoregressive models, PRESS perturbation

1 | INTRODUCTION

Resolving how species in a community interact with each other and respond to environmental change is a fundament of community ecology, and multivariate autoregressive (MAR) models provide one approach to do so. MAR models originally gained traction as “Vector Autoregressive Models” in econometrics (Lutkepohl, 2005; Sims, 1980), to account for temporal dependencies between time series, predict responses to economic shocks, and infer prediction-based causality (Detto et al., 2012; Granger, 1969). In neuroscience, they are used to reveal connectivity between brain regions (Harrison, Penny, & Friston, 2003; Rogers, Katwal, Morgan, Asplund, & Gore, 2010; Seth, Barrett, & Barnett, 2015). In ecology, they are applied to infer species “interaction strength,” a crucial but multifaceted notion in community ecology (see Novak et al., 2016; Wootton & Emmerson, 2005) which in a broad sense represents the intra- and interspecific net effects of species abundances on population growth rates. Their use is also advocated to identify environmental drivers of community dynamics (Fischer, Frost, & Ives, 2001; Francis et al., 2012; Hall et al., 2009; Hampton et al., 2008; Huber & Gaedke, 2006; Klug, Fischer, Ives, & Dennis, 2000; Lindegren, Möllmann, Nielsen, & Stenseth, 2009; Mac Nally et al., 2010; Scheef, Hampton, & Izmet'eva, 2013), to predict the fate of communities submitted to environmental changes (Cooper, Spencer, & Bruno, 2015; Gross & Edmunds, 2015; Ives, 1995; Ives, Carpenter, & Dennis, 1999), or extract measures of community stability and resilience (Britten et al., 2014; Gross & Edmunds, 2015; Ives et al., 1999; Klug & Cottingham, 2001; Lindegren et al., 2010). This broad use of MAR models in ecology arises from the connection of MAR(1) models (with lag of one time-step) to mathematical models of community dynamics (Ives, Dennis, Cottingham, & Carpenter, 2003). Today, MAR modelling has been brought to a general audience thanks to the design of user-friendly R packages (Hampton et al., 2013; Holmes, Ward, & Wills, 2012; Holmes, Ward, & Scheuerell, 2014), and even though most of the early MAR applications in ecology focused on lake or marine systems, the approach has also taken up in terrestrial ecology (Almaraz & Oro, 2011; Mutshinda, O'Hara, & Woiwod, 2009).

MAR(1) models offer to ecologists a practical tool to study time series that is also well rooted in ecological theory, as they can be viewed as a first-order approximation of unknown, nonlinear dynamics around a stable equilibrium (Ives et al., 2003). Hence, MAR(1) models can be fitted to a large number of systems whose underlying dynamics are unknown, as long as stationarity can be safely assumed for the time series at hand. Once fitted, MAR(1) models are essentially a multispecies Gompertz dynamics (Dennis & Taper, 1994; Ives et al., 2003; Supporting Information S1). In a

Gompertz competition model, the expected growth for a given species at times $t+1$ is a linear function of its \ln -density and of the \ln -density of its competitors at times t . The linear assumption of the Gompertz model is convenient when it comes to model fitting (Ives, 1995) because growth rates are expressed in a logarithmic scale. However, density-dependencies other than Gompertz are likely to occur in real systems, for example, when trophic relationships are involved as we have no mechanistic predator-prey model with Gompertz density dependence. Yet, very little is known regarding the robustness of MAR(1) models to departures from \ln -linearity in the underlying, data-generating dynamics. In his seminal paper, Ives (1995) provided some answers regarding the robustness of MAR(1) models to departures from \ln -linearity, using a model of three competing prey following a Lotka-Volterra type dynamics with Ricker density-dependence and of one predator with a type II functional response. As Ives (1995) stated, the simulated example was “moderately complex and therefore presented a considerable challenge to the prediction techniques.” The results were encouraging, proving that meaningful predictions could be obtained for such a system. However, general conclusions cannot be drawn from a single simulated experiment with a single parameter set and model structure. A thorough evaluation is currently critically needed, as the applications of MAR modelling in community ecology are increasing, while there is a controversy regarding the usefulness of linear approximations for unravelling ecological dynamics from observed time series. On the one hand, MAR(1) models are still the base for recent methodological developments in high-dimensional models (Ovaskainen et al., 2017), while on the other hand, some studies have suggested that linear autoregressive approaches may be inappropriate to model nonlinear ecological dynamics and have proposed alternative nonlinear fitting approaches to infer species interactions (Sugihara et al., 2012; Suzuki, Yoshida, Nakanishi, & Fukuda, 2017).

This study therefore provides a thorough evaluation of the performance of MAR(1) models when fitted to unknown nonlinear dynamics. To do so, we first briefly review the basic formulation and assumptions of MAR(1) models. We then show how a wider range of models of ecological communities relate to MAR(1), by addressing an array of nonlinear stochastic models representing competitor, predator-prey, and host-parasitoid interactions, as well as a larger food web. The nonlinearities we explore occur in the form of nonlinear self regulation such as in Ricker or Beverton-Holt models, possibly leading to overcompensatory dynamics with Ricker, and as nonlinear functional responses in enemy-victim models (predator-prey or host-parasitoid systems). For each model, we present equilibria and Jacobian matrices to demonstrate how these models link to the MAR(1) formulation. To

test the robustness of fitted MAR(1) models to nonlinearities in ecological dynamics we extensively sample the parameter space of each model to produce a large set of simulated time series of interacting species subjected to three different levels of process error to which we fit a MAR(1) model. From these, we evaluate the capacity of the fitted MAR(1) model to (1) provide information about the ecological processes at play in the underlying ecological dynamics, (2) infer interaction strengths and approximate the underlying community dynamics, (3) predict short-term dynamics as well as long-term changes induced by altered mean environmental conditions.

2 | MATERIALS AND METHODS

2.1 | MAR(1) theory

A detailed description of the formulation of MAR(1) models and how they connect to more mechanistic models derived from ecological theory is provided in Supporting Information S1, sections 1 & 2. The standard equation for a MAR(1) model describing the dynamics of a vector \mathbf{x} of time series is:

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

This equation can be interpreted as a multispecies Gompertz competitive community dynamics, in which \mathbf{x} are species ln-abundances, the vector of intercept \mathbf{a} corresponds to the zero ln-density growth rate; the matrix \mathbf{B} relates to the intra- and interspecific competition coefficients, \mathbf{C} corresponds to the environmental effect on species growth rates and \mathbf{w}_t is a multivariate-normally distributed error vector with mean $\mathbf{0}$ and variance-covariance matrix Σ .

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 nonlinear, stochastic function of 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 abundances \mathbf{n}^* and for environmental variables standardized to mean $\mathbf{0}$ simplifies to:

$$\mathbf{x}_{t+1} \approx \mathbf{J}\mathbf{x}_t + \mathbf{Q}\mathbf{u}_t \quad (2)$$

where \mathbf{x} now represents the deviation of ln-abundances from equilibrium ($\mathbf{x}_t = \mathbf{n}_t - \mathbf{n}^*$), \mathbf{J} is the Jacobian matrix of partial derivatives with respect to species ln-abundances and \mathbf{Q} is the matrix describing the effect of the environment on species growth rates modelled as $\mathbf{r}_t = \mathbf{r} + \mathbf{Q}\mathbf{u}_t$. By comparing equation (1) and (2) it is clear that \mathbf{B} corresponds to \mathbf{J} , \mathbf{C} corresponds to \mathbf{Q} and that the intercept vector \mathbf{a} is a zero vector, since the ln-abundances are centred around the equilibrium point. In community ecology, \mathbf{J} is often referred to as the community matrix (although the term “community matrix” encompasses other forms, see Novak et al., 2016) and can be used to define interaction strengths. The ln-transformation before centring

of the species abundance data is essential to the stochastic context because the process error on population growth rates is generally ln-normal (Royama, 1992) and all the theory for MAR(1) models is developed for Gaussian process error.

2.1.1 | Short-term forecasts and long-term predictions following environmental “PRESS” perturbations

A fitted MAR(1) model such as Equation 1 can be directly applied to predict species ln-abundances for the next time step, given that current ln-abundances and covariates are known. Such forecasts can support management and conservation of natural populations (Ward, Holmes, Thorson, & Collen, 2014). They are obtained under the constraining assumption that the system is at its dynamic equilibrium, that is, the means of the stationary distributions of species ln-abundances and environmental covariates remain constant through time.

MAR(1) models can also be used to predict the fate of the community over longer periods, in response to a change in the mean of the environmental covariates (i.e. a “PRESS” perturbation Bender, Case, & Gilpin, 1984). Such change could be, for example, a sudden and sustained increase in temperature. From the mean stationary distribution of \mathbf{x}_t at equilibrium derived from Equation 1 (Ives, 1995; Klug & Cottingham, 2001), the expected change in species equilibrium ln-abundances following an environmental perturbation $\Delta_u = \mathbf{u}_2 - \mathbf{u}_1$ becomes

$$\Delta \mathbf{x}^* = (\mathbf{I} - \mathbf{B})^{-1} \mathbf{C} \Delta_u \quad (3)$$

Equation 3 provides a simple formulation to predict long-term changes in species ln-abundances following environmental change, explicitly disentangling changes due to species interactions in $(\mathbf{I} - \mathbf{B})^{-1}$ from changes due to environmental forcing $\mathbf{C} \Delta_u$.

2.2 | Simulating ecological dynamics

Because we focus on how nonlinearities affect the performance of fitted MAR(1) models when analysing community dynamics, we used low-dimensional, 2-species systems, to explore in detail the consequences of disregarding such nonlinearities. In addition, we also considered a larger food web (see Supporting Information S2 for details). We used six 2-species, discrete-time models to simulate ecological dynamics (Table 1). Three competition models were implemented with either Gompertz, Ricker or Beverton–Holt density dependence. Prey–predator dynamics was simulated with the Lotka–Volterra model, with and without a type II functional response. Lastly, host–parasitoid dynamics was simulated with the May–Hassell model (Hassell, 2000; May, 1978). Without stochasticity, each but one of these models displays a stable equilibrium point. The Lotka–Volterra model with type II functional response can be parameterized to produce either a stable equilibrium point or a stable limit cycle, and we treated both separately.

TABLE 1 Name, ecological significance, and values of all parameters used in our data-generating models. LVR : Lotka-Volterra model in discrete-time with Ricker density-dependence; LVR-T2, same model with a Type II Holling functional response instead. Min and max values refer to the bounds of the uniform distribution used for parameter simulation

Model	Notation	Ecological meaning	Min value	Max value
Common to all models	q	Environmental effect on species 1 growth rate	0.01	0.5
Gompertz	α_{11}	Intraspecific competition for species 1	0.01	1.9
	α_{12}	Competitive effect of species 2 on species 1	0.01	0.5
	α_{21}	Competitive effect of species 1 on species 2	0.01	0.5
	α_{22}	Intraspecific competition for species 2	0.01	1.9
	r_1	Zero-log-density growth rate for species 1	0.5	2
	r_2	Zero-log-density growth rate for species 2	0.5	2
Ricker	α_{11}	Intraspecific competition for species 1	0.01	1.9
	α_{12}	Competitive effect of species 2 on species 1	0.01	0.5
	α_{21}	Competitive effect of species 1 on species 2	0.01	0.5
	α_{22}	Intraspecific competition for species 2	0.01	1.9
	r_1	Intrinsic growth rate for species 1	0.5	2
	r_2	Intrinsic growth rate for species 2	0.5	2
Beverton-Holt	α_{11}	Intraspecific competition for species 1	0.01	1.9
	α_{12}	Competitive effect of species 2 on species 1	0.01	0.5
	α_{21}	Competitive effect of species 1 on species 2	0.01	0.5
	α_{22}	Intraspecific competition for species 2	0.01	1.9
	r_1	Intrinsic growth rate for species 1	0.1	5
	r_2	Intrinsic growth rate for species 2	0.1	5
LVR	α	Intraspecific competition for species 1 (prey)	0.01	0.9
	r	Intrinsic growth rate for species 1 (prey)	0.5	2
	γ	Predator (species 2) attack rate	0.01	0.5
	ε	Predator (species 2) assimilation efficiency	0.1	0.5
	μ	Predator (species 2) mortality rate	0.1	0.8
LVR-T2	h	Handling time of prey items by the predator	0.01	0.1
May-Hassell	r	Intrinsic growth rate of the host	0.5	2
	c	Number of female parasitoids sprouting from host	0.01	0.9
	b	Searching efficiency by the parasitoid	0.01	0.5
	l	Aggregation parameter for the parasitism distribution	0.01	0.9

In each model, stochasticity was introduced in the species growth rate as $r_t = r + qU_t + w_t$, where $w_t \sim N(0, \sigma^2)$ and U_t represents an external environmental driver with a moderately complex autocorrelation structure (AR(5) model, including some autocorrelation over several timesteps, see Supplementary Information S3 for how to generate plots of the simulations) exerting some control on species growth. In each model, only species 1 was affected by the environmental variable ($q = 0$ for species 2). To study the effect of the intensity of process error on the robustness of MAR(1) models, we considered three scenarios. Process error on species 1 was set to be either negligible ($\sigma_1^2 = 0.01$), on par with the strength of the environmental signal ($\sigma_1^2 = 0.1$) and well above it ($\sigma_1^2 = 0.5$). For species 2, process error was kept fixed at the intermediate level ($\sigma_2^2 = 0.1$). Such range of process error matches what is observed in the field

(Dennis, Desharnais, Cushing, Henson, & Costantino, 2001; Jonzén, Pople, Grigg, & Possingham, 2005).

2.2.1 | Gompertz competition

The discrete-time Gompertz 2-species competition model (see Supporting Information S1, section 3.1 for a complete description) serves as a control in our study as its parameters show a perfect mapping with the fitted coefficients of a MAR(1) model. The equilibrium ln-abundances derived from Equation 1 are $n_1^* = \frac{\alpha_{12}r_2 - r_1\alpha_{22}}{\alpha_{21}\alpha_{12} - \alpha_{11}\alpha_{22}}$ and $n_2^* = \frac{\alpha_{21}r_1 - r_2\alpha_{11}}{\alpha_{21}\alpha_{12} - \alpha_{11}\alpha_{22}}$, and the Jacobian matrix is:

$$J = \begin{pmatrix} 1 - \alpha_{11} & -\alpha_{12} \\ -\alpha_{21} & 1 - \alpha_{22} \end{pmatrix}. \quad (4)$$

Because all Jacobian elements relate directly to one single parameter of the Gompertz model, the elements of a **B** matrix from a fitted MAR(1) model can be interpreted ecologically in terms of intra- and interspecific competition strengths.

2.2.2 | Ricker competition

As Ives et al. (2003); Ives, Einarsson, Jansen and Gardarsson (2008), we use a 2-species competition model with Ricker density dependence to mimic Lotka–Volterra competition in discrete time (Supporting Information S1, section 3.2). For simplicity, we refer to it as the “Ricker competition” model, leaving the Lotka–Volterra denomination for Prey–Predator models (see next section). The Ricker competition model differs from the continuous time version and from the Beverton–Holt dynamics (see eqs. 17–21 in Supporting Information S1) by its ability to promote cycles and chaos at high growth rates. This system has equilibrium densities $n_1^* = \ln\left(\frac{\alpha_{12}r_2 - r_1\alpha_{22}}{\alpha_{21}\alpha_{12} - \alpha_{11}\alpha_{22}}\right)$ 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 is:

$$\mathbf{J} = \begin{pmatrix} 1 - \alpha_{11}e^{n_1^*} & -\alpha_{12}e^{n_2^*} \\ -\alpha_{21}e^{n_1^*} & 1 - \alpha_{22}e^{n_2^*} \end{pmatrix}. \quad (5)$$

Now that equilibrium values enter the Jacobian, its elements correspond to a mixture of parameters relating to different ecological processes (here intra- and interspecific competition). This is why fitted **B** matrices are often said to be phenomenological: their elements describes the net effect of one species on another, but because of the mixture it is impossible to link such observed net effect unambiguously to a given ecological process.

2.2.3 | Other ecological dynamics considered

The complete set of derivations of equilibria and Jacobian matrices for the four other ecological dynamics is presented in Supporting Information S1. The third competition model used, Beverton–Holt (Supporting Information S1, section 3.3), is usually more stable than its Ricker counterpart (Kot, 2001) but displays a more intricate Jacobian. We also simulated three types of Lotka–Volterra type predator–prey dynamics. In the first (“LVR”) the prey had Ricker density-dependence and the predator consumed prey and died at fixed rates (Supporting Information S1, section 3.4). An important feature of this model is that prey equilibrium abundance is not affected by its growth rate (Supporting Information S1), and hence the PRESS perturbation imposed on the prey only affects the predator. In the second predator–prey model (“LVR-T2”), the predator has a type II functional response (Supporting Information S1, section 3.5). This model is akin to the Rosenzweig–MacArthur model, but its discrete nature allows for a larger range of dynamical behaviours (e.g. chaos). Depending on its parameterization, the LVR-T2 can either present a stable equilibrium or it can display limit cycles. Because we suspected MAR(1) models might handle the two dynamical behaviours differently, we treated them as two separate models, termed “LVR-T2-point” and “LVR-T2-cycle.” Evaluating how MAR(1) would approximate the dynamics produced by LVR-T2-cycle is of particular interest

as this dynamics violates the assumption of stable equilibrium point. Finally, host–parasitoid dynamics were simulated from the May–Hassell model (Hassell, 2000; May, 1978) (Supporting Information S1, section 3.6). All these models display intricate Jacobian matrices and therefore constitute a real challenge for the MAR(1) model.

Despite their mathematical complexity, these 2-species models may appear as highly idealized representations of ecological systems. Therefore, we also simulated a food web dynamics (12 species, inspired from the Gatun Lake case study, Aufderheide, Rudolf, Gross, & Lafferty, 2013) to complement our study of MAR(1) performances on small modules with a more realistic network context. The modelled food web had 20% connectance and was simulated with Lotka–Volterra–Ricker (LVR) and Gompertz dynamics. The models were parameterized with biological constraints maintaining feasibility of the equilibrium and realistic species abundance distributions (i.e. more abundant basal species and slower dynamics for predators). MAR(1) models were fitted to simulated time series of 800 time steps in order to keep the ratio of information in the data and model dimensionality on par with our 2-species modules (we also fitted the full model to time series of 100 time steps, which neither provided a satisfactory model fit nor was comparable to the two-species numerical experiment, see Section 4.5). The details regarding the set-up, simulation and analysis of this food web experiment are to be found in Supporting Information S2.

2.2.4 | Design of the simulation experiment and MAR(1) model fitting

To generate ecological time series from the simulation models, we first chose parameter values by random draws from uniform distributions, bounded within a realistic range of values (Table 1). We kept only the time series in which both species ln-abundances (before centring) were bounded between -20 and 20 (to avoid vanishingly small and exploding populations), and we considered only feasible attractors (nonnegative equilibrium densities) that resulted in a stable probability distribution of abundance values (point equilibrium or limit cycle). After 1000 burn-in time steps, we recorded abundances and the environmental variable U_t during 100 time steps (Figure 1). Such sample size is on the comfortable side of the range of time series length obtained through annual or seasonal monitoring, but as a sensitivity test, we also used time series consisting of 25, 50 and 200 points. We then fitted a MAR(1) model to this dataset, and stored the estimates and confidence intervals for elements of **B** and of the vector of environmental effects **C**. The MAR(1) models were fitted using the MARSS package (Holmes et al., 2012) in R, with the default EM algorithm. Confidence intervals were computed using the estimated Hessian matrix, or were obtained through parametric bootstrap (as implemented in the MARSS package) if that estimation failed. Parametric bootstrap was not used systematically for computing time reasons, but showed similar results for a tested subset (not shown). For each model structure and process error level for species 1, 1000 simulation experiments were performed with the parameters drawn at random and independently.

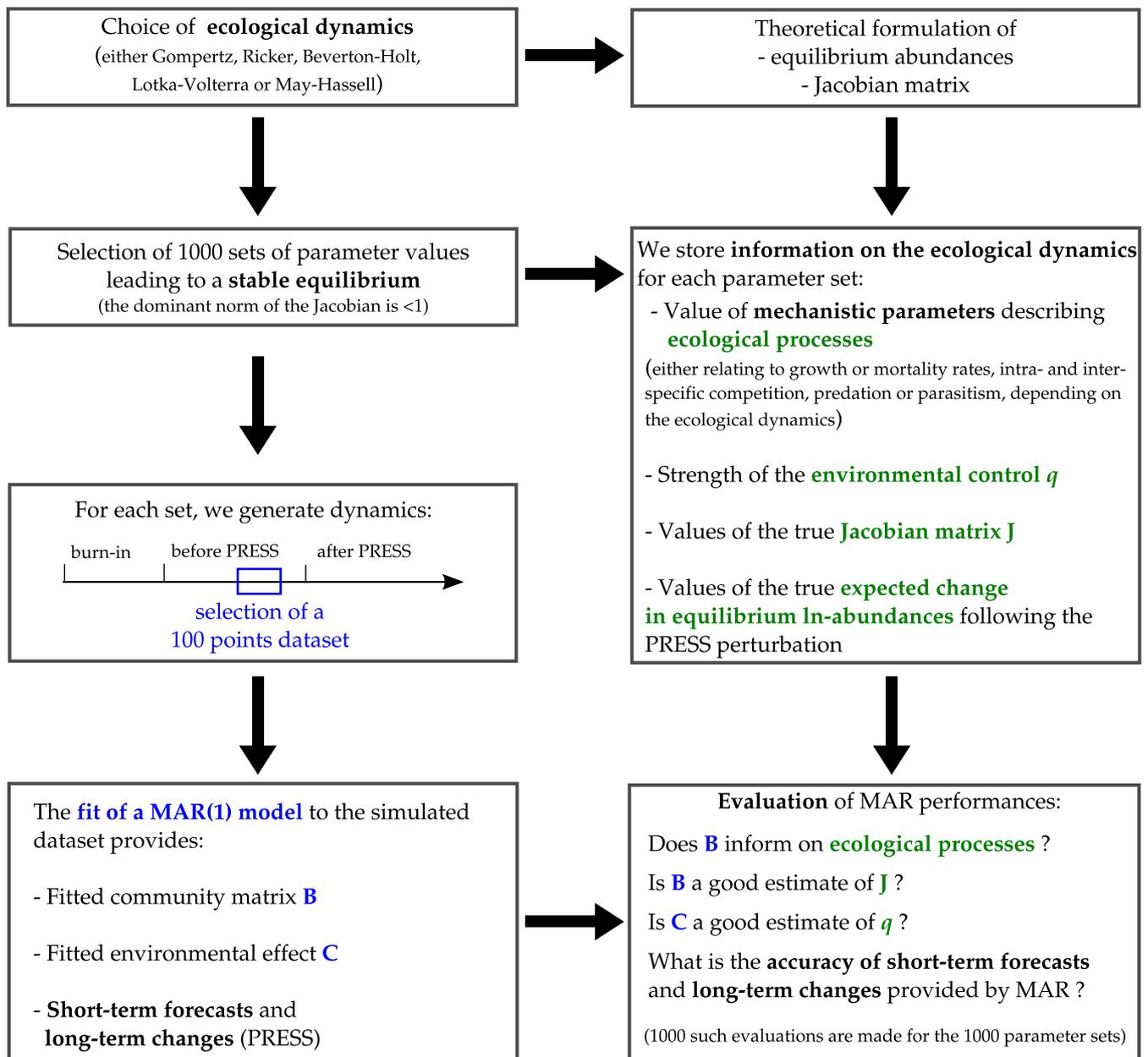


FIGURE 1 Workflow of MAR(1) model evaluation

The R code for fitting MAR(1) models, analysing and plotting the results of the 2-species simulation experiments is provided in Supporting Information S3.

2.3 | Evaluating MAR(1) performances

2.3.1 | How does **B** relate to ecological processes?

As shown previously, the **B** matrix of a fitted MAR(1) model approximates **J** which, in turn, summarizes interaction strengths by blending together parameters describing the ecological processes at work in the underlying dynamics (hereafter denoted “mechanistic parameters”). Except in the Gompertz case, the mapping between **J** elements and the mechanistic parameters of the

underlying dynamics is intricate (Supporting Information S1, section 3). Still, it may be tempting to interpret **B** in ecological terms, and identify its elements e.g. as strength of intra- or interspecific competition, predation or parasitism. Therefore, we evaluate how risky such interpretations may be (when the underlying model is not Gompertz) by identifying the statistical relationships between coefficients of the fitted **B** matrix and the mechanistic parameters.

2.3.2 | How does **B** approximate the Jacobian **J** of the underlying dynamics?

To evaluate how well **B** estimates **J**, we compared the true values of the Jacobian matrix elements (j_{ij}) against their fitted counterparts

(b_{ij}) , using correlations and slopes of linear regression between (b_{ij}) and (j_{ij}) and estimated bias $(b_{ij} - j_{ij})$. From the standard error values provided for each fitted b_{ij} , we estimated how often the true values of j_{ij} lied within the 95% confidence intervals given by the fit of the MAR(1) model. We also reported how often the ranks and signs of \mathbf{B} match the ranks and signs of \mathbf{J} . Finally, we compared the dominant eigenvalue of \mathbf{B} and \mathbf{J} as it is one measure of the system stability and can be interpreted as a return rate to the equilibrium after a perturbation (Ives et al., 2003).

2.3.3 | Do MAR(1) models accurately capture the environmental forcing and provide reliable short- and long-term predictions?

To check for recovery of the environmental effect by the MAR(1) model, we compared the fitted environmental effects c_{11} and c_{12} as well as their 95% confidence intervals to the environmental forcing parameters (q and 0 , as only species 1 is affected by the environment).

We used the Absolute Scaled Error (ASE, Hyndman & Koehler, 2006) on the next point of the simulated data series as a quantitative measure of short-term forecast accuracy. ASE is a scale invariant measure of forecast accuracy that allows comparison across datasets with different scales of variation, is less sensitive to outliers and has already been used to evaluate the forecast accuracy of MAR(1) models, among others, on real time series (Ward et al., 2014). $ASE < 1$ indicates a better forecast, on average, than a naïve one-step forecast which simply considers the last observation as the forecast for the next one. For each model structure, species and process error level, we reported how often the ASE was above 1 across the 1000 simulations. As a qualitative measure of the forecast accuracy, we also reported how often across the 1000 simulations the fitted MAR(1) model would accurately predict the trend of the next point, i.e. whether the next point would lie below or above the last observed value.

Finally, to evaluate the ability of the fitted MAR(1) model to predict the long term effect of a change in environmental conditions, we considered the effect of a PRESS perturbation in which the mean of U_t would shift from 0 to 4 (e.g. mimicking an abrupt temperature increase or eutrophication triggered by nutrient input). True expected long-term change in equilibrium abundances for both species Δn_1^* and Δn_2^* was derived from the species equilibrium abundances provided in Supporting Information S1 for each simulation. They were compared to the predictions Δx_1^* and Δx_2^* from Equation (3) using fitted MAR(1) parameters. For each simulation, we applied parametric bootstrap to Equation 3 by randomly drawing coefficients for \mathbf{B} and \mathbf{C} using means and standard errors obtained from the fitted MAR(1) model. We obtained 1000 predictions and considered that their median was the MAR(1) prediction of the effect of the PRESS perturbation. We finally calculated, from these bootstrapped predictions, the quantile to which the true change corresponded, which characterize the statistical distance between the prediction from MAR(1) and the true PRESS perturbation.

3 | RESULTS

This section reports all the summary statistics of our simulation experiment together with illustrations of the most important results. More detailed results are available in Supporting Information S4, which comprises a set of figures presenting correlations between \mathbf{B} and mechanistic parameters, numerical results regarding the approximation of \mathbf{J} by \mathbf{B} , short-term forecasts, PRESS predictions, and the results of the sensitivity analysis on time series length. Lastly, Supporting Information S5 considers additional scenarios where an observation error is added.

3.1 | How do \mathbf{B} elements relate to mechanistic parameters?

As expected, the mapping between the fitted \mathbf{B} matrix and mechanistic parameters of the underlying dynamics is clear when the underlying dynamics is Gompertz but becomes increasingly challenging with more nonlinear dynamics. The Jacobian matrix for the Lotka–Volterra–Ricker predator–prey model illustrates this blending of mechanistic parameters fairly well (Equation 6, parameters defined in Table 1).

$$\mathbf{J} = \begin{pmatrix} 1 - \frac{\alpha\mu}{\varepsilon\gamma} & -r + \frac{\alpha\mu}{\varepsilon\gamma} \\ \mu & 1 \end{pmatrix} \quad (6)$$

We observe therefore no direct correlation between \mathbf{B} matrix elements and mechanistic parameters, when all are allowed to vary randomly (Table 2, where the results are conditional upon the parameter bounds specified in Table 1). For example, b_{21} represents the net effect of species 1 on species 2. It does correlate to α_{21} , the competitive effect of species 1 on species 2, in both Gompertz and Ricker competitive dynamics. But there is no such correlation between fitted and mechanistic parameters in the case of prey–predator dynamics, the net effect of the prey (species 1) on the predator (species 2) mostly depends on the predator's mortality rate. This is expected from the theoretical formulation of j_{21} (Equation 6 and Supporting Information S1, section 3.4), assuming that the underlying dynamics at play is known. However, for Beverton–Holt and May–Hassell dynamics, the same fitted element b_{21} unexpectedly correlates to the strength of environmental forcing q even though environmental forcing was explicitly accounted for in the MAR(1) model. Similar patterns emerge with other Jacobian elements, for example the fitted intraspecific density dependences b_{11} and b_{22} correlate to intraspecific competition α_{11} and α_{22} in the Gompertz case but relates to intrinsic growth rates otherwise (Table 2). Again, this is not surprising given the importance of the intrinsic growth rate in models with Ricker density dependence. Still, these examples illustrate well that the ecological process(es) to which \mathbf{B} elements relate might not be those we intuitively expect, and that any detailed ecological interpretation of \mathbf{B} matrix elements when the underlying dynamics is unknown can be challenging, and in the worst cases, misleading.

TABLE 3 Summary statistics of interaction inference (**B** versus **J**) for the 7 ecological models (in columns) with 2 species

specific question	Data-generating model: process error on species 1:		Compettz		Ricker		Beverton-Holt		LVR-simple		LVR-T2-point		LVR-T2-cycle		May-Hassell							
	evaluation criterion		0.01	0.1	0.5	0.01	0.1	0.5	0.01	0.1	0.5	0.01	0.1	0.5	0.01	0.1	0.5					
			constant J Jacobian value																			
Do B and J correlate ?	Corr. between b_{11} and J_{11}	1.00	0.99	0.99	0.97	0.95	0.85	0.92	0.94	0.92	0.82	0.76	0.50	0.74	0.73	0.38	0.04	-0.21	-0.36			
	Corr. between b_{12} and J_{12}	0.98	0.88	0.65	0.97	0.92	0.76	0.97	0.90	0.73	0.89	0.84	0.53	0.78	0.41	0.70	0.61	0.25	0.88	0.84	0.74	
	Corr. between b_{21} and J_{21}	0.80	0.92	0.97	0.86	0.94	0.92	0.74	0.91	0.95	0.68	0.79	0.72	0.63	0.76	0.74	0.63	0.54	0.54	0.68	constant Jacobian value	
	Corr. between b_{22} and J_{22}	0.99	0.99	0.99	0.95	0.95	0.89	0.88	0.90	0.88	0.23	0.18	0.28	0.17	0.09	0.06	0.11	0.07	-0.38	0.76	0.76	0.75
Is there some systematic bias in the fitted B values ?	median of $b_{11} - J_{11}$	0.01	0.00	-0.01	0.06	0.08	0.11	0.04	0.03	0.04	0.07	0.05	-0.01	0.12	0.12	0.19	0.46	0.50	0.64	-0.01	-0.03	-0.04
	median of $b_{22} - J_{22}$	0.00	0.01	0.02	0.03	0.06	0.13	0.00	0.01	0.02	0.07	0.05	-0.01	0.12	0.12	0.19	0.46	0.50	0.64	0.02	0.06	0.08
	median of $b_{21} - J_{21}$	0.01	0.00	0.00	0.05	0.05	0.05	0.01	0.00	0.00	-0.10	-0.07	-0.07	-0.06	-0.06	-0.07	-0.23	-0.20	-0.07	-0.03	-0.03	-0.04
	median of $b_{12} - J_{12}$	-0.01	-0.02	-0.01	0.03	0.05	0.12	-0.01	-0.01	0.03	-0.04	-0.04	-0.03	-0.04	-0.04	-0.03	-0.03	-0.03	-0.02	0.06	0.07	0.12
Is J within the confidence intervals of B ?	% of J_{11} out of c.i.95% of b_{11}	5.20	4.60	4.90	42.80	38.50	46.90	41.60	28.00	27.50	72.90	56.70	63.70	72.30	57.10	58.20	77.30	65.40	82.10	10.90	13.20	11.80
	% of J_{12} out of c.i.95% of b_{12}	3.50	3.90	5.30	19.60	14.50	20.90	10.80	6.90	9.00	64.20	40.00	20.20	78.00	61.40	52.50	99.50	99.30	96.60	40.40	42.60	43.10
	% of J_{21} out of c.i.95% of b_{21}	5.60	5.00	6.30	18.20	21.50	42.20	10.60	9.90	18.30	34.60	35.40	50.00	26.30	30.50	56.30	93.10	89.70	62.00	13.60	16.40	25.20
	% of J_{22} out of c.i.95% of b_{22}	6.30	6.20	6.20	18.00	25.80	41.10	8.50	7.90	16.90	10.40	10.20	10.50	14.00	16.50	13.30	16.90	13.00	10.80	38.10	49.20	64.90
Do ranks in B values reflect ranks in J values ?	% of j11 correctly ranked	91.50	88.00	83.60	85.70	83.40	76.10	89.90	88.10	87.10	58.90	63.70	44.60	58.50	60.50	56.70	77.40	82.20	57.00	Ties in the Jacobian	Ties in the Jacobian	Ties in the Jacobian
	% of j12 correctly ranked	80.60	78.90	68.50	83.90	79.30	69.30	87.80	85.00	79.20	88.80	89.70	70.80	82.20	82.00	85.20	99.00	97.30	90.30	99.80	99.80	99.90
	% of j21 correctly ranked	75.40	79.40	74.40	79.80	78.00	74.50	78.00	78.70	75.80	66.20	72.30	60.50	68.20	74.60	62.60	86.60	90.50	84.00	98.80	98.80	98.80
	% of j22 correctly ranked	88.30	85.80	84.30	83.10	79.70	74.90	80.60	81.40	81.50	98.60	99.00	99.80	98.70	99.10	99.70	89.90	90.00	63.30	Ties in the Jacobian	Ties in the Jacobian	Ties in the Jacobian
Do signs in B values reflect signs in J values ?	% of j11 correctly signed	98.00	96.90	95.30	93.70	92.40	84.00	97.90	96.90	96.30	76.70	79.30	61.80	80.90	81.30	73.60	99.10	97.70	90.90	100.00	100.00	100.00
	% of j12 correctly signed	98.50	93.90	84.10	96.80	90.20	74.10	97.60	90.70	85.00	97.00	95.90	91.20	93.40	90.30	87.70	99.50	97.80	90.10	100.00	99.80	99.70
	% of j21 correctly signed	92.30	94.50	98.20	85.40	89.40	93.80	78.70	84.10	92.40	98.00	99.60	99.80	94.80	98.30	99.70	99.40	99.00	98.30	100.00	100.00	100.00
	% of j22 correctly signed	96.30	95.30	96.00	92.20	91.30	86.40	86.50	88.70	88.70	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	96.00	97.30	99.60
How do the stability properties of B match the stability properties of J ?	% fitted B having a stable equilibrium	100.00	100.00	100.00	99.90	99.70	99.90	99.70	99.80	99.90	99.10	99.30	98.30	98.20	98.00	98.70	97.20	98.50	98.40	100.00	100.00	100.00
	Corr. between max. eigen. of B and J	0.96	0.94	0.93	0.76	0.67	0.60	0.92	0.90	0.86	0.62	0.64	0.41	0.57	0.53	0.33	0.09	0.01	0.09	0.93	0.90	0.83

Subjective color scale:

Best performing cases	Fairly Good	Some Issues	Less performing cases	irrelevant
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3.2 | How do **B** elements relate to net interspecific interactions and intraspecific population regulation?

Signs of diagonal **B** matrix elements reflect the presence or absence of overcompensation (negative in case of overcompensation), while signs of off-diagonal elements give the directions of the net effects of the interspecific interactions. We considered sign recovery to be successful when 90% of simulations gave correct sign ($\text{sign}(B_{ij}) = \text{sign}(J_{ij})$). This was the case for 80% of our scenarios and **B** elements (Table 3). Cases in which sign recovery failed can be split between inter- and intraspecific interactions. First, interspecific interaction signs were slightly less well recovered for nonlinear competition (c. 90% of cases with successful sign recovery, 75% in the worst cases for Ricker and Beverton–Holt Dynamics) than for enemy-victim models (prey–predator and host–parasitoid dynamics), which performed very well (correct sign recovered in >95% of cases). Second, overcompensation, denoted by negative diagonal element in **J**, was present in Ricker competition and LVR model but was not always recovered in the sign of b_{11} (Figure 2a, Table 3). The LVR model performed especially poorly in that respect (<80% of sign recovery, 60% at high process error).

Correlations and slopes of linear regressions suggested close relationships between the values of **B** and **J** elements in Gompertz and Beverton–Holt models, without notable bias (i.e. slopes not different from one, Figure 2, Supporting Information S4 section 2). Such relationships deteriorate in models with Ricker density-dependence, due to a systematic bias with **B** elements and an increase in the variability of the estimates (Figure 2). Concerning the diagonal elements, the strength of over- or undercompensation (intraspecific density-dependence) tends to be underestimated for species 1 in prey–predator models (Figure 2a) and overestimated for species 2 in the May–Hassell model (see Supporting Information S4, fig. 4.5). For off-diagonal elements, underestimation of the magnitude of interspecific interactions was also at play in Ricker-type models (Ricker competition and LVR, LVR-point and LVR-cycle) (Figure 2b, c, Supporting Information S4, Fig. 4.3 and 4.4). Doubling the time series length did not improve how well **B** estimated **J** (Supporting Information S4, section 5). This lack of precision in estimates should, in theory, lead to larger confidence intervals. However, upon examination (Figure 2, Table 3), all models but Gompertz have a large proportion of CIs missing the simulated **J** elements, and more so as time series length increased (Supporting Information S4, section 5). This is especially true for enemy-victim models. As an example, if we average over the three process error levels, 53% of LVR and LVR-T2-point b_{12} CIs did not include the “true” j_{12} value.

Process error also affected whether interspecific interactions were recovered by the MAR(1) model, and additional observation error generally decreased the recovery rate (Supporting Information S5). Figure 2c shows that increasing process error on species 1 led to a better recovery of its effect on species 2 (b_{21}). Conversely, decreasing process error on species 1 improved the estimation of b_{12} (Figure 2b). In other words, increased process error (due to e.g. environmental variance) in the growth rate of the focal species impairs estimation of effects of other species, while increased process errors in the growth rate of other species improves the estimation of their effects on the focal species.

The dominant eigenvalue of **B** was inferior to 1 in more than 95% of cases, even in the presence of data generated by LVR-T2-cycle for which the dominant eigenvalue is greater than 1 by definition. Correlation between the dominant eigenvalue of **B** and **J** was very good for Gompertz, Beverton–Holt and May–Hassell, fairly good in the case of Ricker, LVR and LVR-T2-point and poor with LVR-T2-cycle (Table 3), suggesting that when the underlying dynamics has a stable equilibrium, the MAR(1) approximation is able to reproduce accurately its stability properties *sensu* Ives et al. (2003).

3.3 | Do MAR(1) models accurately capture environmental forcing and provide reliable short- and long-term predictions?

The environmental forcing on species 1 was well captured by MAR(1) models across all data-generating models (Table 4, Supporting Information S4). Qualitative forecasts from MAR(1) models were moderate to fair, with often at least 70% correctly predicted trend for the next unobserved point of the time series (Table 4) but rarely more than 90%. Qualitative forecasts obtained for nonlinear predator–prey models were the less accurate. The results on the accuracy of quantitative short-term forecasts measured by ASE are very similar, with predator–prey dynamics as well as Beverton–Holt competition models not so well predicted by MAR(1). Lastly, process error intensity had a notable negative effect on the accuracy of species 1 forecast with all data-generating models.

PRESS predictions were rather accurate for Gompertz and May–Hassell simulations (Figure 3a,b,e,f, Table 4, fig. S4.6) but more problematic otherwise. In the Ricker (Figure 3c,d) and the Beverton–Holt (fig. S4.6) competition models, future equilibrium ln-abundances of species 1 were strongly and systematically overestimated, while for species 2 they were underestimated. They were, however, mostly in the right direction (>90% of cases for species 1 and >75% of cases for species 2, Table 4). For predator–prey models, in which only the predator's

FIGURE 2 Comparison of fitted **B** elements (y-axis) with their true **J** counterparts (x-axis) for (a) b_{11} , (b) b_{12} , (c) b_{21} and (d) b_{22} . In each panel, rows correspond to the underlying model (from top to bottom: Gompertz, Ricker and LVR) and columns correspond to process error intensity on species 1. Each graph is based on 1000 simulations, each having a unique parameter set for the underlying model. Each dot corresponds to one simulation; blue dots correspond to cases where the true value j_{ij} lies within the 95% confidence interval obtained for b_{ij} from the MAR(1) fit, pink dots display cases where the true value lies outside the 95% confidence interval. The blue line corresponds to the diagonal $y = x$, indicating perfect match. The dashed line shows the actual regression line of $j_{ij} \sim b_{ij}$

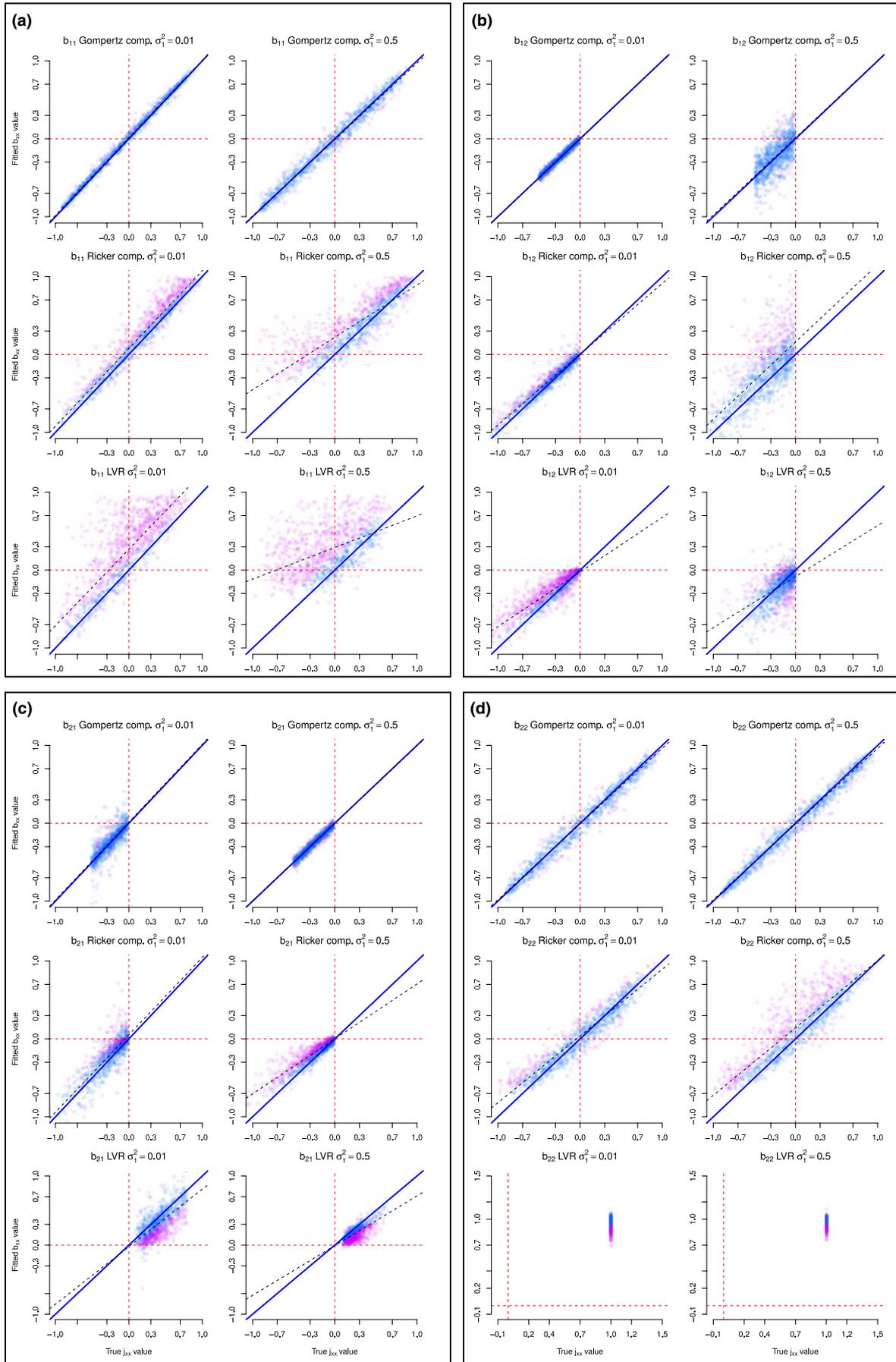


TABLE 4 Summary statistics of environmental effects detection and predictive performance of MAR(1) models, for the 7 ecological models (columns) with 2 species

specific question	Data-generating model: process error on species 1:							evaluation criterion															
	Gompertz		Ricker		Beverton-Holt		LVR-simple		LVR-T2-point		LVR-T2-cycle		May-Hassell										
	0.01	0.1	0.5	0.01	0.1	0.5	0.01	0.1	0.5	0.01	0.1	0.5	0.01	0.1	0.5								
Accuracy of the detection of the environmental effect	% of q_{11} out of c.i.95% of c_{11}	19.90	12.10	8.00	18.70	12.40	7.60	19.40	9.70	6.80	31.10	14.00	10.00	27.50	16.70	9.60	21.40	17.80	11.10	15.30	9.50	8.30	
	% of q_{21} out of c.i.95% of c_{21}	4.90	5.80	4.30	4.90	6.50	6.60	6.60	6.60	6.10	6.80	9.10	7.00	8.00	6.50	7.20	6.90	9.40	8.70	6.50	7.10	8.10	8.20
	% of q_{11} correctly signed	100.00	99.00	97.10	99.90	97.70	90.30	100.00	98.70	94.00	97.00	93.60	77.50	97.50	93.20	80.10	78.10	74.30	74.50	99.90	98.30	96.00	96.00
	median of $c_{11} - q_{11}$	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01	-0.02	-0.02	-0.02	-0.02	-0.02	0.00	-0.01	-0.01	-0.01
	median of $c_{21} - q_{21}$	0.00	0.00	0.00	-0.01	-0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Accuracy of the short-term forecasts	% of well predicted next trend, sp1	90.30	83.50	80.20	87.20	79.10	68.80	84.60	73.80	68.60	79.80	76.30	69.60	76.00	75.20	69.50	74.90	67.70	66.50	90.40	82.50	73.70	73.70
	% of well predicted next trend, sp2	77.50	75.10	79.90	74.50	77.50	76.30	67.00	71.00	72.00	64.20	64.30	62.80	60.00	56.50	61.40	72.20	72.20	63.30	85.30	83.40	88.50	88.50
	% ASE >1, sp1	3.30	12.60	17.90	7.60	22.90	34.10	9.50	23.90	34.40	17.30	33.30	37.60	41.50	38.60	36.50	32.90	28.80	37.20	12.00	9.90	5.00	5.00
	% ASE >1, sp2	22.80	21.90	17.60	22.90	21.40	23.90	35.00	29.40	30.70	37.80	33.30	37.60	41.50	38.60	36.50	32.90	28.80	37.20	12.00	9.90	5.00	5.00
	Correlation between Δx_1^t and Δh_1^t	0.97	0.98	0.96	0.55	0.66	0.63	0.67	0.64	0.53	0.55	0.46	0.46	0.45	0.55	0.45	0.24	0.41	0.33	0.34	0.45	0.40	0.28
Accuracy of the prediction of the PRESS effect	Correlation between Δx_2^t and Δh_2^t	0.89	0.90	0.92	0.53	0.67	0.59	0.46	0.46	0.45	0.55	0.45	0.24	0.41	0.33	0.34	0.45	0.40	0.28	0.89	0.85	0.76	0.76
	Slope of the linear regression $\Delta x_1^t - \Delta h_1^t$	0.91	0.96	0.93	6.78	4.88	4.69	6.13	5.04	4.62	6.78	4.88	4.69	6.13	5.04	4.62	6.78	4.88	4.62	0.91	0.90	0.85	0.85
	Slope of the linear regression $\Delta x_2^t - \Delta h_2^t$	0.67	0.91	0.84	0.39	0.38	0.52	0.21	0.26	0.39	2.06	1.47	0.59	1.62	1.19	1.74	3.12	3.64	3.39	1.12	1.18	1.07	1.07
	% of Δh_1^t out of c.i.95% of Δx_1^t	3.10	3.90	4.50	56.46	40.02	21.62	49.55	34.77	25.73	14.83	9.57	4.68	22.20	15.92	5.88	9.98	10.56	4.07	1.10	1.90	2.70	2.70
	% of Δh_2^t out of c.i.95% of Δx_2^t	1.90	2.90	3.20	10.21	8.23	6.21	20.66	18.44	16.42	14.13	10.07	5.70	13.34	11.02	6.28	16.26	11.88	7.52	25.40	18.50	14.20	14.20
	% of Δh_1^t correctly signed	99.70	98.90	96.70	99.30	97.19	89.59	99.60	98.70	93.69	99.60	98.70	93.69	99.60	98.70	93.69	99.60	98.70	93.69	99.80	97.60	96.50	96.50
	% of Δh_2^t correctly signed	89.20	89.60	88.40	82.58	82.85	79.38	78.84	78.46	80.98	89.81	85.80	71.21	84.73	79.90	73.35	78.60	73.81	66.36	99.90	98.10	96.00	96.00
Subjective color scale:																							
Best performing cases			Fairly Good			Some Issues			Less performing cases			irrelevant											

Species 1 equilibrium is not affected by the press perturbation

Species 1 equilibrium is not affected by the press perturbation

Species 1 equilibrium is not affected by the press perturbation

equilibrium ln-abundance is supposed to change following the PRESS perturbation (cf. Supporting Information S1, sections 3.4 and 3.5), MAR(1) still predicted significant deviations for the prey in up to 20% of the cases (with LVR-T2-point at low process error, fig. S4.6) while the predator's response was in general overestimated (Figure 3h,j,l). Lastly at high process error, the sign of the predator's response could be mis-predicted in up to 30% of simulations (Figure 3j,l, Table 4).

3.4 | Do 2-species results hold in a food web context ?

We observed a notable difference in the correspondence between **B** and **J** for on- and off-diagonal elements (Supporting Information S2), suggesting that net interspecific interaction strengths were less well estimated than net intraspecific interaction strength in such larger webs. There were relatively few differences in MAR(1) performances in terms of interspecific interaction sign recovery between Gompertz and LVR, corroborating our results on 2-species systems that interaction sign recovery is robust to nonlinearities. The underestimation of interaction strength reported for the 2-species LVR was visible at the base of the food web, but not at the upper levels, where the correlations between **B** and **J** were also weaker. Such upper-level interactions were therefore less well estimated, but it is important to note that they were also less strong by construction. This is notably due to the low abundances of the high trophic levels that decrease their Jacobian values. Similarly to the 2-species models, the environmental effects were overall very well recovered when strong enough. Overcompensation was recovered as well. Finally, whereas PRESS-predictions were accurate for 2-species Gompertz model, they were rather poor for both Gompertz and LVR food webs, as errors in estimation of net interactions ripple through the web.

4 | DISCUSSION

By deriving and quantifying the accuracy, bias and predictive ability of fitted MAR(1)-models using simulated data from seven types of competitive, predator-prey and host-parasitoid systems, as well as a larger food web, with nonlinear stochastic dynamics and varying process error levels, we have provided a thorough test of the MAR(1) approach for multispecies dynamics. Our findings illustrate the importance of assuming that the studied system exhibits Gompertz density-dependence for any other inference than interaction sign. This assumption is a stern prerequisite for interpreting numerical values of the MAR(1) interaction matrix **B**. While we can specify mechanistic competition models of the Gompertz type, in most enemy-victim scenarios we cannot, so that **B** elements have to be interpreted in most cases in terms of net interaction strengths blending mechanistic parameters.

Except for diagonal elements in cases of overcompensatory dynamics, high confidence can be put in the sign of **B** elements. Thus, the direction of net interactions in a community can be assessed using MAR(1). Depending on the underlying dynamics at play, however, the magnitude of point estimates and confidence intervals

of **B** may poorly match the actual values of the community matrix **J**. MAR(1) models accurately identified the environmental forcing acting on a species in all types of tested dynamics. Predictions of long-term responses to sustained environmental changes, however, tended to be either over- or underestimated for all but 2-species host-parasitoid and Gompertz systems. In the following sections, we discuss these findings in details, attempt to elucidate the reasons behind discrepancies, and provide some guidance on interpretation and use of MAR(1) models fitted to ecological data.

4.1 | The ecological significance of MAR(1) model parameters

Predictions regarding which **B** elements should be related to which mechanistic parameter could theoretically be made from the formulations of **J** (see Supporting Information S1) but only if the underlying dynamics at play are known. When they are not, zero **B** matrix coefficients should not be interpreted as a lack of ecological interactions between individuals, while nonzero should be interpreted as net interaction strength without a direct relation to the ecological processes at work. Another result important for the interpretation of estimated MAR(1) parameters was the relationship between the strength of the environmental forcing and **B** elements in the Beverton-Holt, LVR-T2-cycle and May-Hassell models. This shows that when the underlying dynamics is not Gompertz, some part of the environmental forcing is passed onto **B** and interpreted by MAR(1) as an interspecific effect, hence contributing to the mismatch in value between **B** and **J**. As the strength of environmental forcing is still rather accurately predicted even for these models, it is however likely that, in our simulations, only a small fraction of environmental forcing is passed onto **B**.

Beyond ecological interpretation, these observations also have implications for model building strategies. Some studies either restrict *a priori* the range of MAR(1) models investigated, or evaluate *a posteriori* the MAR(1) model they obtain according to "ecological plausibility" (Fischer et al., 2001; Hampton, Scheuerell, & Schindler, 2006; Huber & Gaedke, 2006; Ives et al., 1999). An interaction is then said to be plausible when the value of the **B** element can be easily interpreted in ecological terms (e.g. negative interactions between competitors). However, given the often idiosyncratic nature of the relationship between **B** and ecological processes at play in the underlying dynamics (see Supporting Information S1), it might well be that the phenomenological approximation provided by the fit of a MAR(1) model, despite not being "ecologically plausible," is still a better approximation of the net effects among species than another model restricted to supposedly "plausible" auto- and cross-correlations.

4.2 | The Gompertz assumption of linearity on a log-scale

Given its importance for model interpretation, testing the Gompertz assumption should appear common sense—it is after all checking model fit. But it is easier said than done with short ecological time

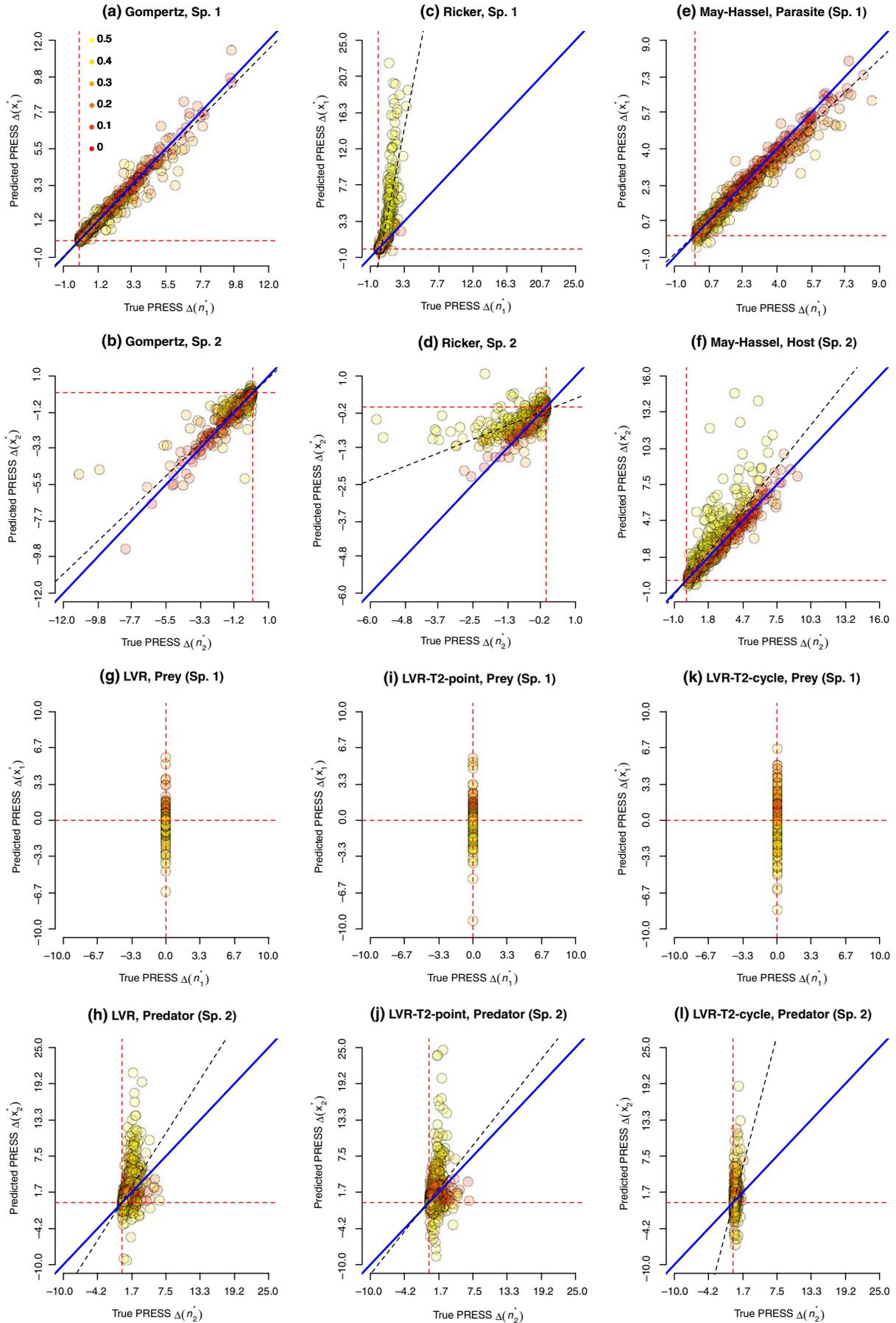


FIGURE 3 Comparison of the median predictions of the species' response to a PRESS perturbation obtained from a fitted MAR(1) model (y-axis) with the actual response in the simulated model (x-axis). Responses are expressed as change in \ln -populations densities. Each plot is based on 1000 simulations, each having a unique parameter set for the underlying model, and each dot corresponds to one simulation. The colourscale for dots (upper-left plot) illustrates the distance between the true change and the median prediction in terms of interquartile range, that is, a value of 0.5 means that the true change lies beyond the 95% prediction interval derived from the bootstrapped distribution of the predictions. The blue thick lines show the perfect ($y = x$) match. The thin dashed lines show the actual regression $y \sim x$

series. Visual examination of residual plots is recommended (Ives et al., 2003; Vik, Brinch, Boutin, & Stenseth, 2008), which we systematically produced during the analysis (Supporting Information S3). At low process error level, these plots often displayed the curved relationships typical of nonlinearities unaccounted for, as exemplified in Figure 4a. As process error increased to levels commonly observed in the field ($\sigma^2 = 0.1$ – 0.5 , Dennis, Kemp, & Taper, 1998; Dennis et al., 2001), these curved relationships became harder and harder to detect, to the point where they could very

well become unnoticed (Figure 4b). Hence, even if looking at the residuals is a crucial step of the modelling process, failing to observe curved relationships is not a proof of absence of nonlinearities, especially for noisy systems. Fitting both linear and nonlinear models to ecological time series can be recommended, even though a bit cumbersome in practice. Comparison between the fitted linear and nonlinear models can provide some insights on the type and importance of nonlinearities existing in the underlying models, which, in turn, controls the amount of information that can be extracted by

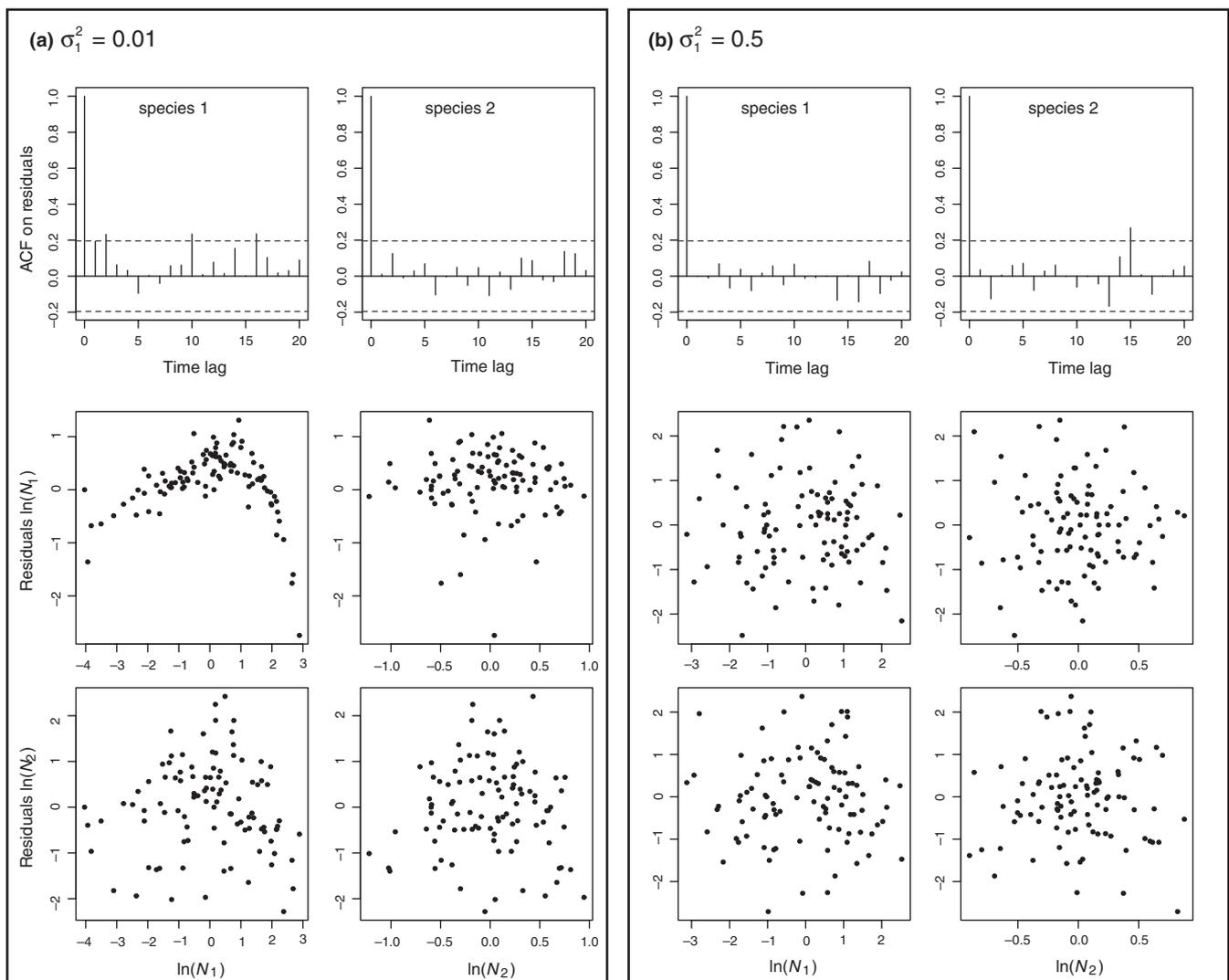


FIGURE 4 Autocorrelation function for the residuals (uppermost panels) and plots of the residuals (y-axis) against species \ln -abundances (x-axis) for two selected simulations of the Ricker model at low (a) and high (b) process error levels. Patterns typical from unaccounted nonlinearities (e.g. curvilinear relationships in the residual plots) are clearly observed in the low-process error simulation, but are much more difficult to detect for the high-process error simulations

a MAR(1) model together with the type and strength of biases that can be expected. As often pointed out (Ives, 1995; Perretti, Munch, & Sugihara, 2013), linear models are so much easier to fit and use than nonlinear models that even in the presence of nonlinearities, their use can be preferred. But, as we demonstrated, knowledge of the type of nonlinearities at work allows to anticipate the biases entailed in the use of a linear approximation.

4.3 | What is the quality of interaction strengths estimates and dynamical approximation offered by a MAR(1) model?

MAR(1) models do provide information on the sign of net effects among species, but do not reliably recover their actual values when the underlying dynamics are nonlinear, as shown by the loss of correlation between \mathbf{B} and \mathbf{J} outside of the Gompertz case. The general expectation is that MAR(1) models pass unexplained variability onto the process error matrix Σ , and they do so; the ratio of fitted versus true process error (Σ_{11}/σ_1^2 and Σ_{22}/σ_2^2) is indeed inflated for all data-generating models but the Gompertz (Supporting Information S4, fig. S4.7). This is good statistical behaviour, as we prefer unexplained variability to be passed onto process error rather than onto other MAR(1) parameters such as biotic interactions, to avoid biased estimates. Still, our results show that such transfer of variability to variance terms does not completely prevent net biotic interactions from getting distorted by underlying nonlinearities.

To understand any ecological system's dynamics, errors on the ranks and signs of the community matrix elements are the most problematic. Overall, these errors are rare, but we identified two situations in which they are more likely to occur. In competitive systems with nonlinear dynamics, the net effect of a competitor on a target species, revealed by off-diagonal \mathbf{B} elements, might be missed when the target species is submitted to strong environmental control. With models presenting density dependence of Ricker type, overcompensation might be missed due to the lack of detection of negative diagonal \mathbf{B} elements. Lastly, many aspects of the mapping between \mathbf{B} and \mathbf{J} are lost when the underlying dynamics have no stable equilibrium and even if this is expected, one should be particularly careful when interpreting or projecting MAR(1) models fitted to such dynamics.

4.3.1 | MAR(1) models and overcompensatory dynamics

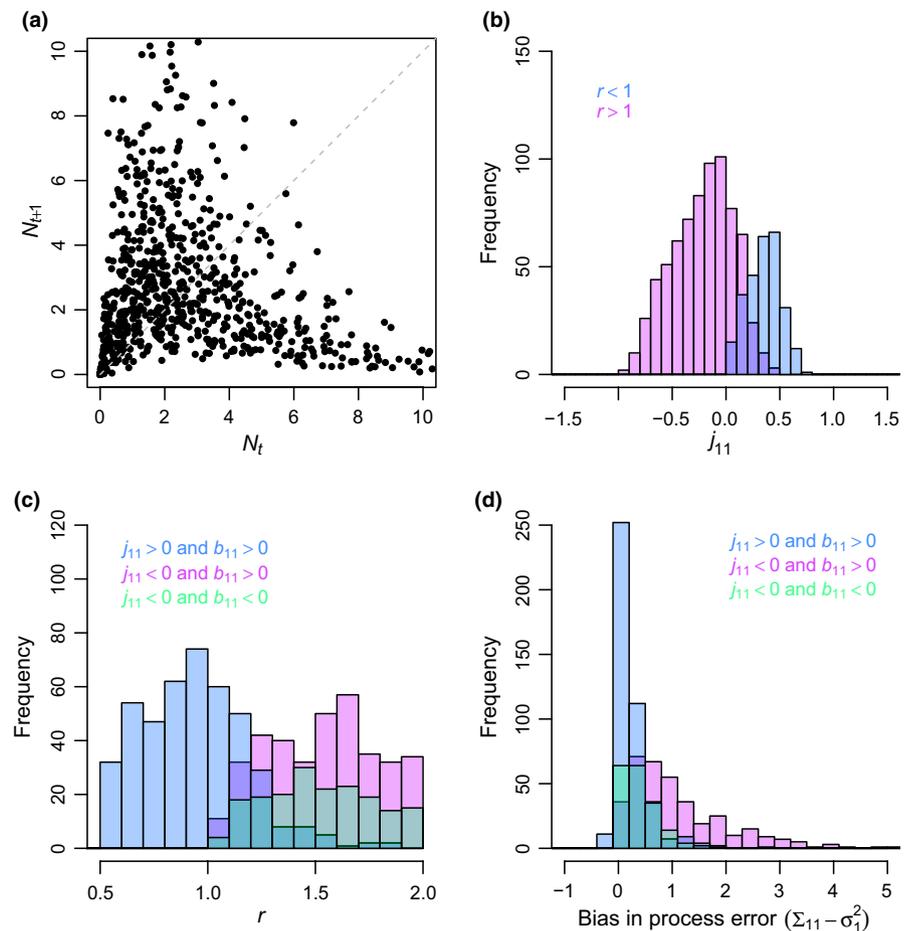
MAR(1) models display in theory overcompensatory dynamics for a species whenever its diagonal \mathbf{B} matrix element is negative. Therefore, observing a negative fitted \mathbf{B} diagonal element is often interpreted as an indication that the corresponding species displays overcompensatory dynamics (Hampton et al., 2013; Ripa & Ives, 2003). However, detecting overcompensation with log-linear models is known to be difficult from previous results on single-species models (Barraquand, Pinot, Yoccoz, & Bretagnolle, 2014). Overcompensation

happens with Ricker dynamics at high intrinsic growth rate. In our Ricker-based data-generating models, overcompensation is expected as soon as the intrinsic growth rate r becomes superior to 1 (Kot, 2001, Supporting Information S1, section 3.4). This is also the case with most simulations from the LVR model, even though the dynamics is complexified by predation (Figure 5a): negative values on the Jacobian diagonal also relate to simulations with higher intrinsic growth rate for the prey (Figure 5b). Since both MAR(1) and LVR models show overcompensation when \mathbf{B} or \mathbf{J} diagonal elements are negative, one can reasonably expect that overcompensation in the LVR model should be picked-up by fitting a MAR(1) model. However, only a third of negative j_{11} values had their fitted counterpart b_{11} also negative (Figure 5c), which means that MAR(1) models often missed overcompensation when it was present. Detecting overcompensation is an important aspect of studying ecological dynamics. It allows, for example, for better anticipation of biases in population viability analysis (Sabo, Holmes, & Kareiva, 2004). Faulty assumptions about the shape of density dependence, combined with overcompensatory intrinsic population dynamics, can lead to strongly biased estimated effects of autocorrelated covariates, especially when autocorrelation is negative (Linden, Fowler, & Jonzén, 2013). The reasons for which overcompensatory dynamics would be picked up by MAR(1) models in some cases, but not in others, is unclear and would require further work. Still, we observed that in cases when overcompensatory dynamics were missed, fitted process error Σ_{11} was systematically inflated (Figure 5d), most likely because unaccounted variability due to overcompensatory dynamics is passed onto the process error. Hence, when one suspects that overcompensation is at play in a time series fitted by a MAR(1) model, inflated process error could be an indication that the model just missed it.

4.3.2 | Limit cycles

The dominant norms of the \mathbf{B} matrices obtained from fitted MAR(1) models almost always indicated stable dynamics (dominant norm < 1), even when the data-generating model had no stable point. This resulted in a complete mismatch between \mathbf{B} and \mathbf{J} with LVR-T2-cycle, because in that case the dominant norm of \mathbf{J} is above 1 (due to the escape of trajectories from the equilibrium to settle on the limit cycle). This is expected: the fitted MAR(1) model ascribes this dynamical behaviour to the only possible cyclic behaviour it can generate, quasi-cycle with stable equilibrium point. MAR(1) models will systematically produce fixed equilibrium points even if the true attractor is not a point. This emphasizes that stability indicators obtained from a MAR(1) model, which heavily rely on the properties of the estimated \mathbf{B} matrix (Ives et al., 2003), may be more or less appropriate depending on the type of attractors. In cases such as limit cycles, the mapping from \mathbf{B} to \mathbf{J} is severely distorted, which in turn limits the interpretation one can make from stability indicators. Testing for the existence of a single equilibrium point, or at least investigating the consequences of their absence, is therefore an important step when attempting to derive stability measures from MAR(1) model fit (see for example Britten et al., 2014), and can be achieved by fitting alternative nonlinear models to data (Ives et al., 2008).

FIGURE 5 Recovery of overcompensation. (a) For one simulation of the LVR model in which $r = 1.96$, relationship between prey density at times t (x-axis) and $t + 1$ (y-axis). The scatterplot displays the curvilinear pattern typical from overcompensation. (b) statistical distribution of j_{11} for the LVR model, when the underlying dynamics of the prey has low ($r < 1$, blue) and high ($r > 1$, red) growth rate. Most j_{11} values are negative in the latter case. (c) Statistical distribution of r across 1000 LVR simulations, spread between three cases: When the sign of j_{11} was correctly predicted by b_{11} either positive (blue) or negative (green), and when negative j_{11} would not be recovered in b_{11} (red). (d) Statistical distribution across 1000 LVR simulations of the bias on the process error, spread between the same cases as in (c). Mismatch between the signs of j_{11} (negative) and b_{11} (positive) lead to inflated Σ_{11} . These results are extracted from the set of simulation experiments in which simulated process error on species 1 σ_1^2 was set to 0.5



4.4 | The predictive performance of MAR(1) models

Fitted MAR(1) models produced a meaningful short-term forecast in roughly three cases out of four for competitive and host–parasitoid dynamics, which in our view constitutes a reasonable performance. One should expect a slight decrease in MAR(1) forecast accuracy with nonlinear predator–prey systems and high process error. This echoes the study of Ward et al. (2014) in which a poorer forecast accuracy with log-linear autoregressive models, among other methods, was evidenced for highly variable time series.

Long-term PRESS predictions, on the other hand, can provide robust information on the direction of species' responses, but not on their magnitude. In case of competition models, overestimation of the change in species 1 ln-abundance could be surprisingly severe, up to a factor 100. This is due to how intraspecific regulation acts in the underlying dynamics. In a single population following a Gompertz dynamics, the population increase in ln-abundance from one time step to another is a linear function of intraspecific ln-abundance, $n_{t+1} - n_t = r - \alpha n_t$. The equilibrium ln-abundance in this case is simply $\frac{r}{\alpha}$ and the expected change in equilibrium ln-abundance following a PRESS perturbation P is $\frac{\alpha}{\alpha} \times P$, that is, a linear function of the PRESS scaled by intraspecific regulation. If intraspecific regulation is nonlinear, for example, as in the Ricker model $n_{t+1} - n_t = r - \alpha e^{n_t}$, the expected change in equilibrium ln-abundance following a PRESS perturbation is $\ln\left(1 + \frac{\alpha P}{r}\right)$, that is, a

ln-linear function of the PRESS mediated by the species' growth rate. Hence, predicting the PRESS effect as a linear function when it actually is ln-linear can result in a major bias. The same reasoning, albeit more complex analytically, applies to our competition- and predator–prey systems in which intraspecific regulation follows either the Ricker or the Beverton–Holt form. Therefore, it is probably safe to assume that in any ecological systems in which the growth function of the population decreases nonlinearly with density, the predicted effect of a PRESS perturbation on that population will, depending on whether the PRESS is positive or negative, most likely be either over- or underestimated, respectively, by a fitted MAR(1) model.

Biased PRESS predictions can have strong implications for management. In the fisheries context, MAR(1) models have been used to investigate the effect of PRESS perturbations (fishing intensity, Lindegren et al., 2009, and climate forcing, Lindegren et al., 2010) in the Baltic Sea, with conclusions regarding the levels of sustainable fishing of cod. Fishing release on cod is similar to the environmental PRESS in our simulations: it has a positive effect on population growth rates. As the system considered therein cannot be related to Gompertz dynamics in a mechanistic sense (it includes prey–predator relationships instead of competition, and encompasses several trophic levels), the resulting PRESS predictions potentially overestimate the effect of fishing release, which suggests that avoidance of collapse could be more likely in MAR(1) than in reality. Other studies have used log-linear MAR(1)

models to predict the responses of coral reefs to climate change (Cooper et al., 2015; Gross & Edmunds, 2015), we advise to do so with caution when only one type of density-dependence is considered.

4.5 | Complexifying our experiment: Observation error and food web models

In this study, we used mainly 2-species models because they allow to vary broadly the parameter space and they constitute a suitable starting point to foster understanding, by analytical derivation of Jacobian matrices \mathbf{J} of the underlying dynamics and comparison to community matrices \mathbf{B} in MAR(1)-models. As we focused primarily on the type of nonlinearities at play, other topics such as the inclusion of observation errors, the colour of environmental noise or systems of higher dimensionality are open avenues for further study. We have nonetheless made some progresses regarding observation errors and high dimensionality.

4.5.1 | Observation error

Adding observation error to stochastic discrete-time dynamics has been already investigated by Lindén and Knape (2009) who suggested possible biases in the detection of environmental effect when observation errors were not accounted for while present. On the other hand, there are a number of identifiability issues when including observation errors without prior knowledge of their magnitude (Auger-Méthé et al., 2016; Knape, 2008). For some of our data-generating models (Gompertz, Ricker and Beverton–Holt), we added various levels of observation errors both to our simulations and to the fitted MAR(1) models (Supporting Information S5). Our results confirmed the identifiability problems already encountered by others: when neither observation error nor process error is set to a fixed value, some of the observation error can be transferred to the process error—or vice-versa—sometimes to a large extent (fig. S5.1). Our recommendation is therefore to include observation error only when prior knowledge of its magnitude exists, and if this knowledge can be used to constrain model fit (see S5 for details).

4.5.2 | From small modules to networks

Results from our food web numerical experiment confirmed our 2-species results: the robustness of interaction sign inference to nonlinearities holds in higher dimensional systems of similar information content/parameters ratio. This last point is of importance: because of the increase in the number of MAR(1) parameters fitted to a food web, time series length had to be significantly extended to allow for a reasonable MAR(1) fit. That time series length constrains the estimation of MAR(p) models is one of the basic tenets of econometrics and time series statistics (Lutkepohl, 2005); in this paper, we assumed time series long enough that we know the MAR(1) models can by themselves be estimated, if no additional nonlinearities are considered. Fitting the food web model to time series showed clearly, for instance, that time series longer than 100

need to be considered (see Supplementary Information S2) or additional sparsity constraints have to be implemented (see below). We investigated the robustness of our results to time series length T by repeating our simulation experiment for $T = 25, 50,$ and 200 points, in the 2-species models. We observed that interaction sign inference remains remarkably good for those other lengths, but the short-term predictive ability declines when T declines (Supporting Information S4, Section 5). As an empirical rule, we suggest that time series length should be at least 5 times greater than the number of a priori nonzero elements in \mathbf{B} in order to correctly recover interaction signs. In other words, we propose to satisfy $T/(n^2(1-s)) > 5$, in which n is the number of species and s the proportion of zeroes in the \mathbf{B} matrix.

Many challenges remain to thoroughly evaluate the application of MAR(1) models to food webs. A key issue where much statistical progress is ongoing is model selection in high-dimensional systems (Basu & Michailidis, 2015; Charbonnier, Chiquet, & Ambroise, 2010; Michailidis & d'Alché Buc, 2013; Mutshinda, O'Hara, & Woiwod, 2011; Ovaskainen et al., 2017), where the number of potential parameters almost always outgrow the size of the dataset (this would have occurred even with 12 species for $T = 100$). Regularization (Basu & Michailidis, 2015) or dimension reduction (Ovaskainen et al., 2017) techniques may allow to fit large MAR(1) models to shorter time series than we do here, though we believe that a proper evaluation of interaction (sign) recovery may require stricter evaluation criteria than those currently employed (see Supporting Information S2).

A sometimes neglected issue that becomes even more important as assumptions on web topology are introduced for model fitting (e.g. sparsity, latent variables structuring \mathbf{B}), is that the underlying topology of the interaction web is never fully known. Thus, close attention should be paid to the consequences of mis-specifying the topology of net interaction strength prior to MAR(1) fitting, and how robust MAR(1) model estimations are to increases in the proportion of hidden players (e.g. nonmonitored species or forcing factors, an old yet vexing problem of community ecology; see Schaffer, 1981).

5 | CONCLUSION

By closely examining the link between different types of nonlinear community dynamics and MAR(1)-approximations thereof, we aimed to promote an appreciation of how MAR(1) models work in practice, as well as their (inevitable) limitations. MAR(1) models are powerful tools to make sense of noisy community time series, approximate community dynamics, make short-term predictions and infer the signs of species net interaction strengths. This flexibility makes them a premium tool for ecologists. However, our study shows that not accounting for existing nonlinearities in the underlying dynamics (1) weakens the inference that can be made from MAR(1) to mechanistic parameters, (2) impairs estimation of the values of net effects among species, and even distort the approximation of \mathbf{J} to the point that overcompensation or net interspecific interactions can be missed (for nonlinear predator–prey or competitive dynamics, respectively), (3) decreases predictive performances, especially for long-term (PRESS) predictions

of responses to altered environmental conditions when species exhibit self-regulating dynamics and (4) inflates process error estimates (or both process and observation error estimates if both are modelled), especially when the underlying dynamics have no stable equilibrium.

When applying MAR(1) to time series, we therefore recommend to identify possible sources of nonlinearities as a companion modelling effort. Not necessarily to find a replacement for the MAR(1) model - the technical difficulties of fitting nonlinear models are well known, and they often make the fit of a simpler linear model the better option; but, having information on the type of nonlinearities possibly at play in the underlying dynamics can help to interpret the output of the linear model fit, and, based on the results herein, predict the consequences of not accounting for them. If strong nonlinearities are expected, a possible solution is to fit models in which temporal dependence is extended over more than one time step [e.g. ARMA(p,q) models (Ives, Abbott, & Ziebarth, 2010) and their multivariate counterparts], as some nonlinearities can be expressed as time lags (Turchin, 2003). However, with more than one time lag in a multispecies context, the connection with theoretical models could become even more difficult, so the gains in inferential and predictive performance would have to be weighted by the costs in terms of model interpretation.

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AUTHORS' CONTRIBUTIONS

G.C., F.B. and A.G. conceived the ideas and designed methodology; G.C. and F.B. derived the equations in S1, GC performed the main numerical experiments on the 2-species modules, F.B. performed the food web numerical experiment (S2). G.C. led the writing of the manuscript with extensive input from F.B. and A.G. All authors contributed critically to the successive drafts and gave final approval for publication.

DATA ACCESSIBILITY

The R code for running the main simulation experiment is available on FigShare: <https://doi.org/10.6084/m9.figshare.6127877.v1> (Certain, 2018). The R code for running the food web experiment is available on GitHub: https://github.com/fbarraquand/MAR_food-Web_MEE. The associated DOI for the food web experiment is as follows: DOI:10.5281/zenodo.1218024

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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