Comparison Between Lotka-Volterra and Multivariate Autoregressive Models of Ecological Interaction Systems

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Running Headline:

Comparison of Lotka-Volterra and MAR models

Abstract:

1. Lotka-Volterra (LV) and Multivariate Autoregressive (MAR) models are computational frameworks with different mathematical structures that have both been proposed for the same purpose of extracting governing features of dynamic interactions among coexisting populations of different species from observed time series data.

2. We systematically compare the feasibility of the two modeling approaches, using four synthetically generated datasets and seven ecological datasets from the literature.

3. The overarching result is that LV models outperform MAR models in most cases and are generally superior for representing cases where the dependent variables deviate greatly from their steady states. A large dynamic range is particularly prevalent when the populations are highly abundant, change considerably over time, and exhibit a large signal-to-noise ratio. By contrast, MAR models are better suited for analyses of populations with low abundances and for investigations where the quantification of noise is important.

4. We conclude that the choice of either one or the other modeling framework should be guided by the specific goals of the analysis and the dynamic features of the data.

Key words:

Algebraic Lotka-Volterra Inference (ALVI), Lotka-Volterra models, Multivariate Autoregressive (MAR) models, community dynamics, parameter estimation, population dynamics, structure inference, systems biology.

Availability of algorithms used:

https://github.com/LBSA-VoitLab/Comparison-Between-LV-and-MAR-Models-of-Ecological-Interaction-Systems

1. Introduction

The growth of populations has been a topic of human interest since prehistoric times: Babylonian clay tablets documented exponential growth in cuneiform lettering as early as about 4,000 years ago (Sachs & Goetze, 1945; Savageau, 1979). The quantitative representation and analysis of population dynamics is also one of the early roots of mathematical modeling in biology. In the mid-1920s, Alfred Lotka (Lotka, 1925) studied periodic increases and decreases in the populations of lynx and hare in Canada, while Vito Volterra (Volterra, 1926) independently analyzed fish catches and the competition among populations in the Adriatic Sea. Since these early days, Lotka-Volterra (LV) models have become a mainstay—and typical default—in computational ecology (May, 2001) .

With the discovery of complex microbiomes and their surprisingly strong effects on human health and the environment, the interest in interactions among different species has received renewed attention (Gavin, Pokrovskii, Prentice, & Sobolev, 2006; Stein et al., 2013; Shenhav et al., 2019). As an example, we recently inferred the temporally changing interactions among bacterial communities in different lake environments with over 12,000 Operational Taxonomic Units (OTUs) (Dam et al., 2016; Dam et al., 2020). We chose as our computational framework an LV model, which we augmented with LV equations for environmental variables that affected the OTUs (see also (Stein et al., 2013)). Our rationale for this choice was a combination of (1) the successful history of LV models, (2) their mathematical simplicity and tractability and (3) the important fact that parameter values (and thus signs and strengths of interactions) can be obtained from time series data of OTU abundances with methods of linear regression (Voit & Chou, 2010).

Multivariate Autoregressive (MAR) models were proposed a few decades ago as a viable alternative to LV models. Originally proposed for problems in economics (Sims, 1980), Ives suggested their use for predicting responses of populations to environmental changes (Ives, 1995). His specific motivation was to establish techniques for studying how population abundances change in response to long-term environmental trends and for partitioning different factors driving changes in mean population densities in response to these trends. Since this early work, MAR models have been chosen to represent the interaction dynamics between biotic and abiotic drivers, infer the intra- and interspecific effects of species abundances on population growth rates, identify environmental drivers of community dynamics, predict the fate of communities submitted to environmental changes and extract measures of community stability and resilience. The latter was initially applied to lake and marine systems and later in terrestrial ecology (Certain, Barraquand, & Gårdmark, 2018).

Thus, two modeling frameworks with entirely different structures have been proposed for essentially the same purpose of extracting key features of dynamic interactions among coexisting populations of different species from observed time series data. Both methods have had successes, but a direct comparison of the two approaches has not been reported. Such a comparison is the subject of this article.

LV are ODE models, whereas MAR are statistical models. The former were designed to elucidate the long-term dynamics of interacting populations, whereas the latter were conceived to also describe the stochastic structure of a dataset. Our focus for their comparison is the ability of each model structure to produce an acceptable fit to the available data and to capture the process dynamics underlying the observed trends in population abundances.

We use four versions of MAR: MAR without any data transformation, MAR with log transformation, MAR upon data smoothing and MAR with log transformation upon data smoothing. Log transformation is necessary for comparing the general mathematical interpretation of a MAR model with a typical ecological interpretation, where they can be viewed as multispecies competition models with Gompertz density dependence (Ives, 1995; Certain et al., 2018) (Section 1.3 of the *Supplements*). Data smoothing is explored to assess if the advantages of LV models are in fact due to this preparatory step. It is clear that data smoothing will impede the ability of MARs to describe stochastic structures in the data, but this aspect is not the focus of this study.

We begin with a description and comparison of the main features of LV models and MAR models, subsequently analyze small synthetic systems, which offer the advantage of simplicity and full knowledge of all model features, and then assess several real-world systems. It is quite evident that it is impossible to compare distinct mathematical approaches with absolute objectivity and without bias (Rykiel, 1996), and it sometimes happens that inferior choices of models in specific cases outperform otherwise superior choices. We will attempt to counteract these vagaries by selecting case studies we consider representative and by stating positive and negative facts and features as objectively as possible.

2. Materials and Methods

2.1. Lotka-Volterra models

Lotka-Volterra (LV) models (Lotka, 1925; Volterra, 1926) are systems of first-order ordinary differential equations (ODEs) of the format

$$\frac{dX_{i,t}}{dt} = a_i X_{i,t} + \sum_{j=1}^{n} b_{ij} X_{i,t} X_{j,t}, \quad i = 1,2,\dots, n. \qquad \text{eqn 1}$$

The left side of equation 1 represents the change in species X_i with respect to time. The equation with only the first term on the right side, $a_i X_{i,t}$, yields exponential growth, while the sum captures interactions between pairs of populations. Most of these terms represent interactions between different species, such as predation, competition for the same resources or cooperation, but one term in each equation, $b_{ii} X_{i,t} X_{i,t}$, accounts for interactions among the members of the same species and is sometimes interpreted as "crowding effect." Background and further details regarding these models are presented in *Supplements*

Section 1.1. Because ODEs are natural representations of dynamic processes, the index t is usually omitted.

2.2. Estimation of LV Parameters Based on Slopes of Time Courses

Any of the numerous generic parameter estimation approaches for systems of nonlinear ODEs may be used to estimate the parameter values of LV systems; reviews include (Mendes & Kell, 1998; Wedelin & Gennemark, 2007; Chou & Voit, 2009). Here, we use a combination of smoothing, slope estimation, and parameter inference, for which we use the recently introduced Algebraic Lotka-Volterra Inference (ALVI) method (Voit *et al.*, 2021). We begin by smoothing the raw time series data in order to reduce noise in the data as well as in their slopes, where the effects of noise are known be exacerbated (Knowles & Renka, 2014). Many options are available, but smoothing splines and local regression methods are particularly useful (Cleveland, 1981); they are reviewed in *Supplements* Section 1.2.1. Splines have degrees of freedom and we will refer to a spline with, say, 8 degrees of freedom as “8DF-spline”.

The estimation of slopes allows us to convert the inference problem from one involving ODEs into one exclusively using algebraic functions. This conversion is accomplished by substituting the left side of equation 1 with estimated slopes that correspond to values to the dependent variables on the right side, which leaves the parameters as the only unknowns (Voit & Savageau, 1982; Varah, 1982; Voit & Almeida, 2004; see also *Supplements* Sections 1.2.2. and 1.2.3.).

After the differentials are replaced with estimated slopes, two options permit the inference of the parameter values of LV-models. We can apply simple multivariate linear regression (ALVI-LR), where we either use all datapoints or iterate the regression several times with subsets of points, which is a natural approach of creating ensembles of solutions. As an alternative, if n is the number of variables, one may use *n*+1 of the datapoints and slopes, which results in a system of linear equations that can be solved with simple algebraic matrix inversion (ALVI-MI). For a thorough description of the ALVI method please see (Voit et. al., 2021) and an example in *Supplements* Section 1.2.4.

2.3. Multivariate Autoregressive (MAR) models

In contrast to the ODEs of the LV format, Multivariate Autoregressive (MAR) models are discrete recursive linear models. They have the general format

$$X_{i,t+1} = \alpha_i + \sum_{j=1}^{n} \beta_{ij} X_{j,t} + \sum_{g=1}^{m} \gamma_{ig} u_{g,t} + w_{i,t};\ i = 1,2,\dots,n;\quad w_{i,t} \sim N(0,\delta_i) \quad , \qquad \text{eqn 2}$$

where $u_{g,t}$ are environmental variables and $w_{i,t}$ represents normally distributed noise. This set of equations, for different *i*, is usual represented in the matrix form

$$\boldsymbol{X}_{t+1} = \boldsymbol{\alpha} + \boldsymbol{\beta}\boldsymbol{X}_t + \boldsymbol{\gamma}\boldsymbol{u}_t + \boldsymbol{w}_t,\quad \boldsymbol{w}_t \sim MVN(0,\delta). \qquad \text{eqn 3}$$

Explained in words, the "state" of the system at time *t*+1, expressed by the vector $\boldsymbol{X}_{t+1}$, depends exclusively on the state of system one time unit earlier, $\boldsymbol{X}_t$, as well as on external inputs and stochastic environmental effects. Furthermore, α is the vector of intersects and $\boldsymbol{\beta}$ is one row of the population interaction matrix. The term $\boldsymbol{\gamma}\boldsymbol{u}_t$ describes how cofactors affect the dependent variables. Specifically, $\boldsymbol{u}_t$ is a vector of external variables and $\boldsymbol{\gamma}$ is the vector of weights associated with these external variables. Finally, the term $\boldsymbol{w}_t$ is a vector representing stochastic noise affecting the dependent variables. Background and further details regarding these models are presented in *Supplements* Section 1.3.

2.4. Parameter estimation for MAR

Software packages for the estimation of MAR model parameters greatly facilitate the use of these models. An example is the package MARSS, which uses an expectation maximization algorithm (Holmes, Ward, & Wills, 2012; Holmes, Ward, & Scheuerell, 2020). Some details of MARSS are discussed in in *Supplements* Section 1.4. and in the next section.

2.5. Structural Similarities between Modeling Formats

Although LV and MAR models have both been proposed for characterizing the interactions among populations within a mixed community, they are distinctly different in structure and appearance. Nonetheless, they also exhibit fundamental mathematical similarities, which are sketched below; a detailed analysis is presented in *Supplements* Section 1.5.

To assess these similarities, we focus on models without environmental factors, and thus on

$$X_{i,t+1} = \alpha_i + \sum_{j=1}^{n} \beta_{ij} X_{j,t} + w_{i,t};\ i = 1,2,\dots,n;\quad w_{i,n} \sim N(0,\delta_i). \qquad \text{eqn 4}$$

We also suppose that the MAR variables represent the logarithms of abundances, as proposed in (Dennis & Taper, 1994; Ives, 1995; Certain *et al.*, 2018). Borrowing the principles of solving ODEs with Euler's method, we discretize the LV model, which yields

$$X_{i,t+h} = X_{i,t} + h \cdot \frac{dX_i}{dt}\bigg|_{X_i = X_{i,t}} = X_{i,t} + h \cdot X_{i,t}\left(a_i + \sum_{j=1}^{n} b_{ij} X_{j,t}\right), \qquad i = 1,2,\dots,n. \qquad \text{eqn 5}$$

If the dynamics remains close to the steady state, then $X_{i,t+1} - X_{i,t} \approx 0$ for any given *t*. Substituting this approximation into equations 4 and 5 yields

$$\alpha_i + \sum_{j=1}^{n} \beta_{ij} X_{j,t} + w_{i,t} - X_{i,t} \approx 0 \qquad \text{eqn 6}$$

and

$$a_i + \sum_{j=1}^{n} \tilde{b}_{ij} X_{j,t} - X_{i,t} \approx 0, \qquad \text{eqn 7}$$

respectively. Ignoring the noise term in the MAR model, the two sets of near-steady-state equations 6 and 7 are the same if $\alpha_i = a_i$, $\beta_{ij} = b_{ij}$ for all $i \neq j$ and $\beta_{ij} = b_{ij} + 1$ for $i = j$. Thus, the MAR and LV models are mathematically equivalent at the steady state and similar close to it.

3. Results

The comparison between LV and MAR models may be executed in two ways. A purely mathematical approach was sketched in Section 2.5. An alternative approach focuses on practical considerations and actual results of inferences from data. It is described in the following.

For simplicity, we omit environmental inputs ($c_i X_i U_t$ and $\gamma_i u_t$, respectively) and begin by testing several synthetic datasets with different dynamics. We suppose that these data are moderately sparse and noisy, to mimic reality. In particular, we test whether the LV inference from synthetic LV data returns the correct interaction parameters and whether the MAR inference from synthetic MAR data does the same. Subsequently, we test to what degree LV inferences from MAR data yield reasonable results and *vice versa*. Finally, we apply the inference methods to real data. As the main metric, we compare the sums of squared errors and use a Wilcoxson rank test to assess the significance of the difference.

3.1. Case study 1: Synthetic LV data

The first case consists of data that were generated with a four-variable LV model and superimposed with synthetic, normally distributed noise (for details, see *Supplements* Section 2). We also generate a smaller noisy dataset, which however comes with replicates. The specific question we address is whether the LV and MAR inference methods return the true dynamics and parameter values.

The fits for the noisy and replicate LV datasets are presented in Figures 1 a, b, along with parameter estimates. These generally possess the correct sign and could, if deemed beneficial, serve as the starting point for an additional, refining optimization, for instance with a steepest-decent method. The inferred and true values are quite similar for the replicate dataset. By contrast, the parameter values inferred for the noisy dataset do not exactly recoup the true values. In fact, these inferences yield slightly better fits to the noisy data (SSE=17.981) than the "true" values (SSE=18.197), due to the noise. Because we usually obtain better results through ALVI-MI, we display those results here and ALVI-LR results in the *Supplements*.

Figure 1 also displays the MARSS estimates with and without log-transformation of the data and with or without data smoothing. With respect to X_1, X_2 and X_3, these estimates are of adequate quality. They present good fits, although not as good as the LV inference, which is probably not surprising as the data were generated with an LV system. MARSS did not perform well for the "detached" variable X_4, especially for the noisy dataset.

	Initial cond.	Noisy est.	Rep. est.
X1	1.2	1.22856	1.15231
X2	0.3	0.49236	0.36543
X3	2	1.78728	1.75958
X4	0.001	0.03667	0.00116
	True Pars	Noisy est	Rep. est
a1	0.044	0.84002	0.08831
b11	-0.08	-0.71141	-0.09004
b12	0.02	0.38667	0.02142
b13	0.08	-0.04179	0.05606
b14	0	0.02936	0.00001
a2	0.216	-1.14191	0.25503
b21	-0.04	1.15907	-0.08654
b22	-0.08	-0.68274	-0.05206
b23	0.04	0.00876	0.03404
b24	0	-0.07094	0.00701
a3	0.116	14.40459	0.04626
b31	-0.16	-12.78112	-0.08782
b32	0.16	7.23029	0.16915
b33	-0.08	-0.84681	-0.18931
b34	0	0.62883	0.01812
a4	0.2	-2.36404	0.18856
b41	0	2.12859	-0.06477
b42	0	-1.14437	0.03365
b43	0	0.11408	0.06941
b44	-0.1	-0.16695	-0.10442
Degrees of freedom		5, 8, 11, 5	5, 6, 8, 8
Points Sample		8, 13, 17, 19, 79	11, 18, 26, 33, 60

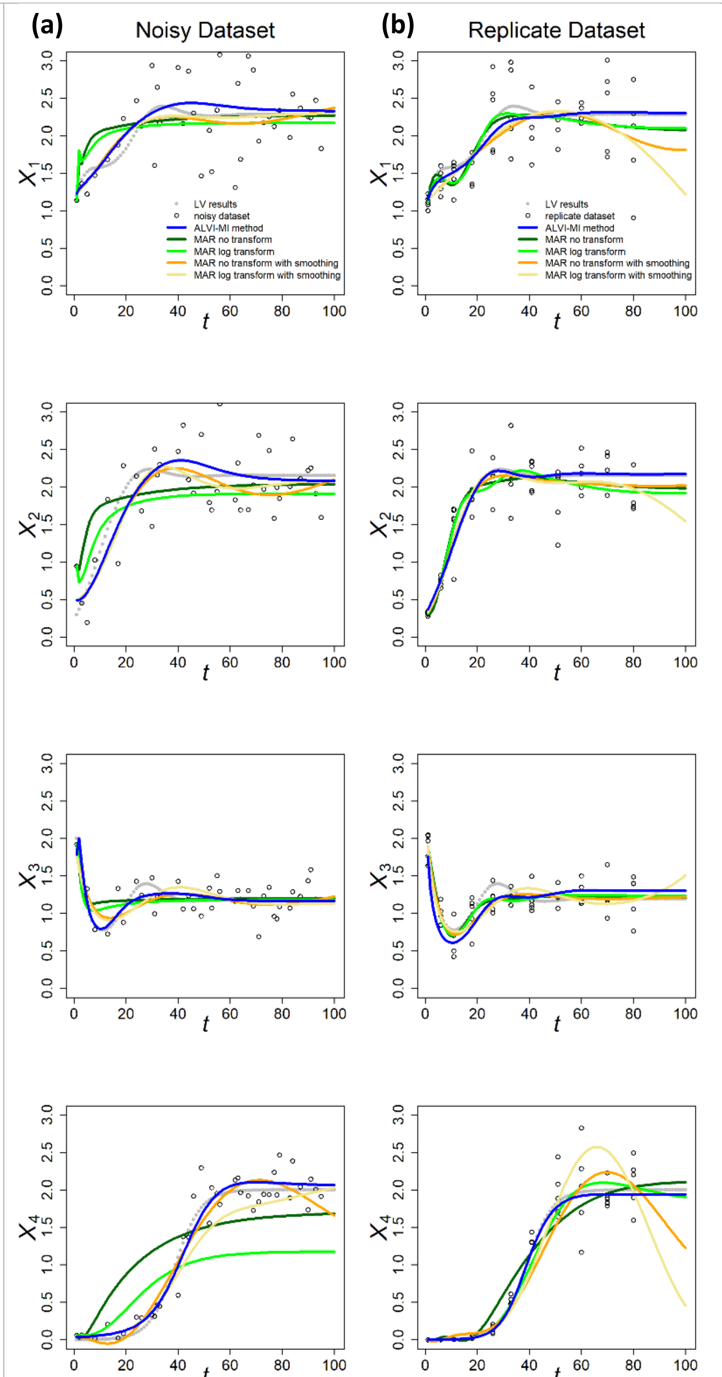

Figure 1: ALVI-MI and MARSS methods applied to noisy (a) and replicate (b) LV datasets. Original synthetic data are shown as gray dots and data with added noise as black circles. ALVI results are presented in blue .True parameters and ALVI-MI estimates are presented in the Table. MAR estimates are presented in green, orange and yellow. Data and parameter estimates for MAR can be seen in Table S1. SSEs for all fits are presented in Table 1 toward the end of the article.

Because MARSS yields parameter values for a discrete recursive system, they are not directly comparable to the true parameters of a LV system; nonetheless, their numerical values are recorded for completeness in Tables S1.4 and S1.5.

For MARSS inferences from the replicate dataset we had to average points with the same time value. MARSS did not converge for all parameters but it still presented a relatively good fit. Additional details are presented in *Supplements* Section 2.

The ALVI-MI method also works well for more complicated dynamics, as demonstrated in *Supplements* Section 2 and Figure S5.

3.2. Case study 2: Synthetic MAR data

Here we reverse the set-up of Case Study 1 by creating synthetic data with an MAR model and test whether either method can infer results corresponding to the original system.

As a representative example, we use a four-variable MAR system to create 31 synthetic datapoints. We create a *noisy MAR* dataset by adding noise in the form of a random normal variable of mean zero and a standard deviation of 20% of each variable's mean to the original 31 points sample. We also create a *replicate MAR* dataset by choosing 12 points and generating 5 replicates by multiplying their values by a random normal of mean 1 and standard deviation of 0.2. The initial conditions, parameters, dynamics, ALVI and MAR fits are presented in Figure 2. All fits to the synthetic MAR data are satisfactory. The LV parameters are not directly comparable to the MAR parameters.

Noisy MAR

Pars	True Values	MAR	MAR log transform	MAR with data smoothing	MAR log transform with smoothing
β11	0.45	0.1326	0.31343	0.39642	0.3582
β21	-0.5	-0.7579	-0.71839	-0.56989	-0.72816
β31	-0.2	-0.3014	-2.56121	-0.04234	-1.47731
β41	0.3	0.0655	0.41855	0.32471	0.3857
β12	0.5	0.4134	0.21377	0.39737	0.29638
β22	0.544635	0.0613	0.97497	0.3656	1.35461
β32	-0.3	-0.2501	2.01907	-0.2907	1.40072
β42	-0.1	-0.0694	-0.75818	-0.14531	-0.59619
β13	-0.1	-0.515	0.00937	0.02061	0.01489
β23	0.3	1.623	-0.02319	1.21771	-0.04951
β33	0.9	0.76	-0.1124	0.96983	0.44232
β43	-0.3	-0.4955	0.0407	-0.03142	0.04829
β14	-0.3	-0.4951	-0.58434	-0.00845	-0.3693
β24	0.1	-0.9279	0.28317	-0.09393	0.8837
β34	0.3	-0.4852	1.51221	-0.10254	3.90492
β44	0.3	0.2066	-0.3689	0.61166	0.15671
α1	2	16.7985	2.91985	1.15325	0.09526
α2	1.02106	42.1023	1.22855	19.75135	0.03591
α3	0.740671	20.7671	-2.84687	8.94758	-0.0315
α4	2	17.8742	5.04906	5.29832	0.00908
δ1	3.320835	9.5406	0.03335	1.17525	0.00537
δ2	4.771945	20.564	0.03175	7.84299	0.00869
δ3	1.214544	8.3144	4.2181	3.09948	0.6299
δ4	3.668288	9.9207	0.05057	1.71729	0.00224

Replicate MAR

Pars	True Values	MAR	MAR log transform	MAR with data smoothing	MAR log transform with smoothing
β11	0.45	0.1313	0.7550	0.4045	0.8751
β21	-0.5	-0.1997	-1.2900	-0.4620	-0.7421
β31	-0.2	0.0452	-0.9240	-0.0046	-0.3758
β41	0.3	0.5716	0.7020	0.3775	0.4040
β12	0.5	0.6439	1.4000	0.3926	0.8919
β22	0.544635	-0.0389	-0.2100	0.0853	0.4392
β32	-0.3	-0.2161	-1.4000	-0.1873	-0.4188
β42	-0.1	-0.2339	0.3570	0.0521	0.1148
β13	-0.1	-1.4212	0.4890	-0.2147	0.5447
β23	0.3	3.2295	-0.7320	2.0833	0.0302
β33	0.9	1.3301	-0.1770	0.9647	0.6010
β43	-0.3	0.5027	0.2900	-0.2409	-0.0582
β14	-0.3	-0.1848	1.6900	0.1292	1.2788
β24	0.1	-0.2463	-2.2500	-1.0586	-0.6291
β34	0.3	-0.0189	-2.4100	-0.1712	-0.3419
β44	0.3	0.5529	1.6100	0.8786	0.9728
α1	1.02106	-0.2209	0.0437	0.2503	0.0305
α2	2	1.8693	0.0597	0.3678	0.0240
α3	0.740671	-0.1895	-0.0261	-0.2918	-0.0320
α4	2	0.0909	-0.0257	-0.1392	-0.0073
δ1	3.320835	0.0029	0.0000	3.2610	0.0060
δ2	4.771945	3.7408	0.0010	10.8861	0.0108
δ3	1.214544	0.0214	0.0018	0.6440	0.0123
δ4	3.668288	0.8913	0.0000	1.9498	0.0038

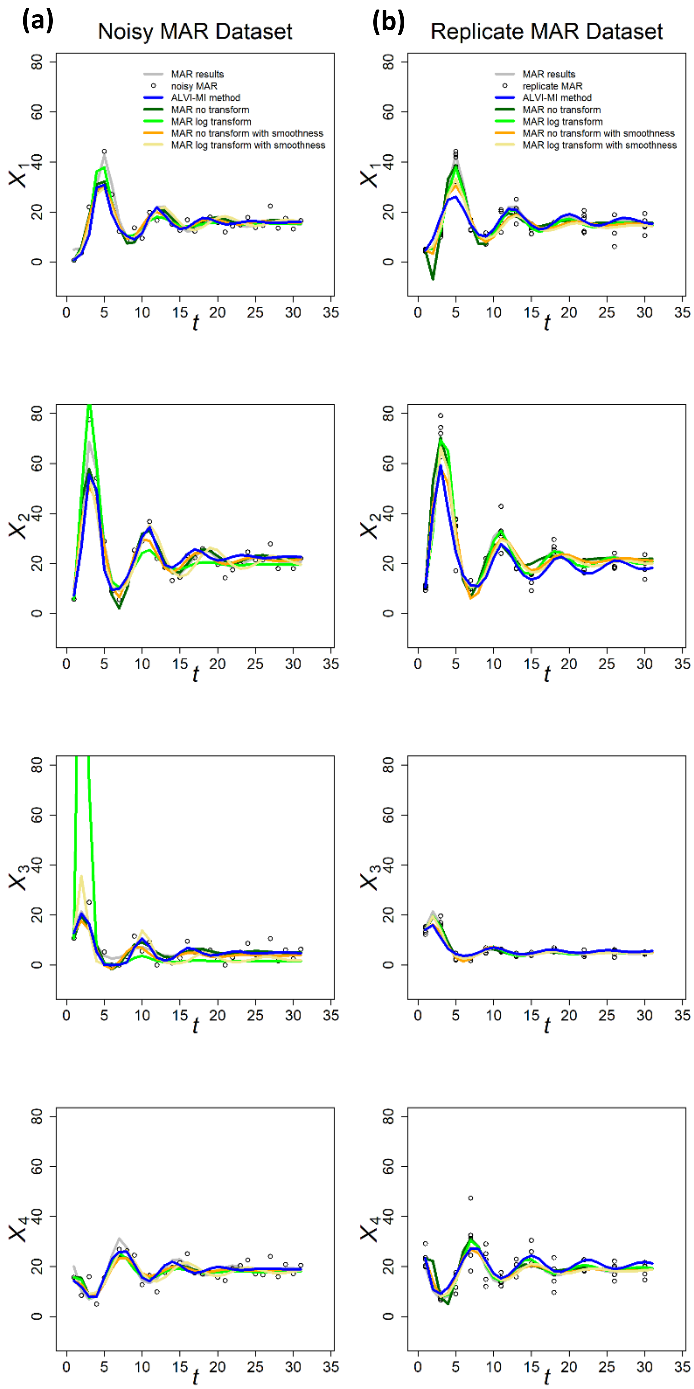

Figure 2: MARSS and ALVI-MI methods applied to noisy (a) and replicate (b) MAR datasets. Original synthetic data are shown as gray dots, data with added noise as black circles. MAR estimates are presented in green, orange and yellow. ALVI results are in blue. The variables of the noisy dataset were smoothed with 15DF-splines and the ALVI-MI solution was calculated with spline points at times 2, 6, 15, 18 and 26. The variables of the replicate dataset were smoothed with 15DF-splines and the ALVI-MI solution was calculated with spline points corresponding

to times 1, 3, 11, 13 and 15. Data and parameter estimates for ALVI can be seen in *Supplements* Table S5. SSEs for these fits are presented in Table 1 toward the end of the article.

In most cases, the different MAR models had difficulties retrieving the true parameters of the system, and sometimes even the correct sign (Figure 2). This is probably due to the small number of datapoints: Certain *et al.* (Certain et al., 2018) suggest that the length of the time series should be at least 5 times greater than the number of *a priori* nonzero elements in the matrix B in order to recover interaction signs correctly. Our sample has 31 observations and should have at least 80. For X_1 and X_4, all models show a similar fit, but not for X_2 and X_3, where MAR models with log transformation show a considerable deviation from the data.

3.3. Case study 3: Experimental data from the literature, previously used for inferences with LV and MAR models

3.3.1. Published LV inferences

Data from Georgy Gause's 1930s experiments and others were recently compiled in the R package gauseR (Mühlbauer *et al.* 2020). In the accompanying paper, the authors present five examples to test their method for estimating LV model parameters. We use the exact same examples to demonstrate to what degree LV and MAR methods are compatible with these real-world data and compare our results to those presented by Mühlbauer and colleagues. For more information regarding the original experimental data, see (Gause, 1934), (Huffaker, Shea, & Herman, 1963) , (McLaren & Peterson, 1994) and (Mühlbauer et al., 2020). The results are presented in Figure 3, with data as symbols and various estimates as lines. SSEs of the different estimates for these and other test examples are presented in Table 1.

The MAR method never outperforms the other methods considered. To be fair, these examples had been used to test actual data for compatibility with the LV structure, which may explain the superior performance of the LV model. Nonetheless, these are the types of data the MAR method is supposed to capture.

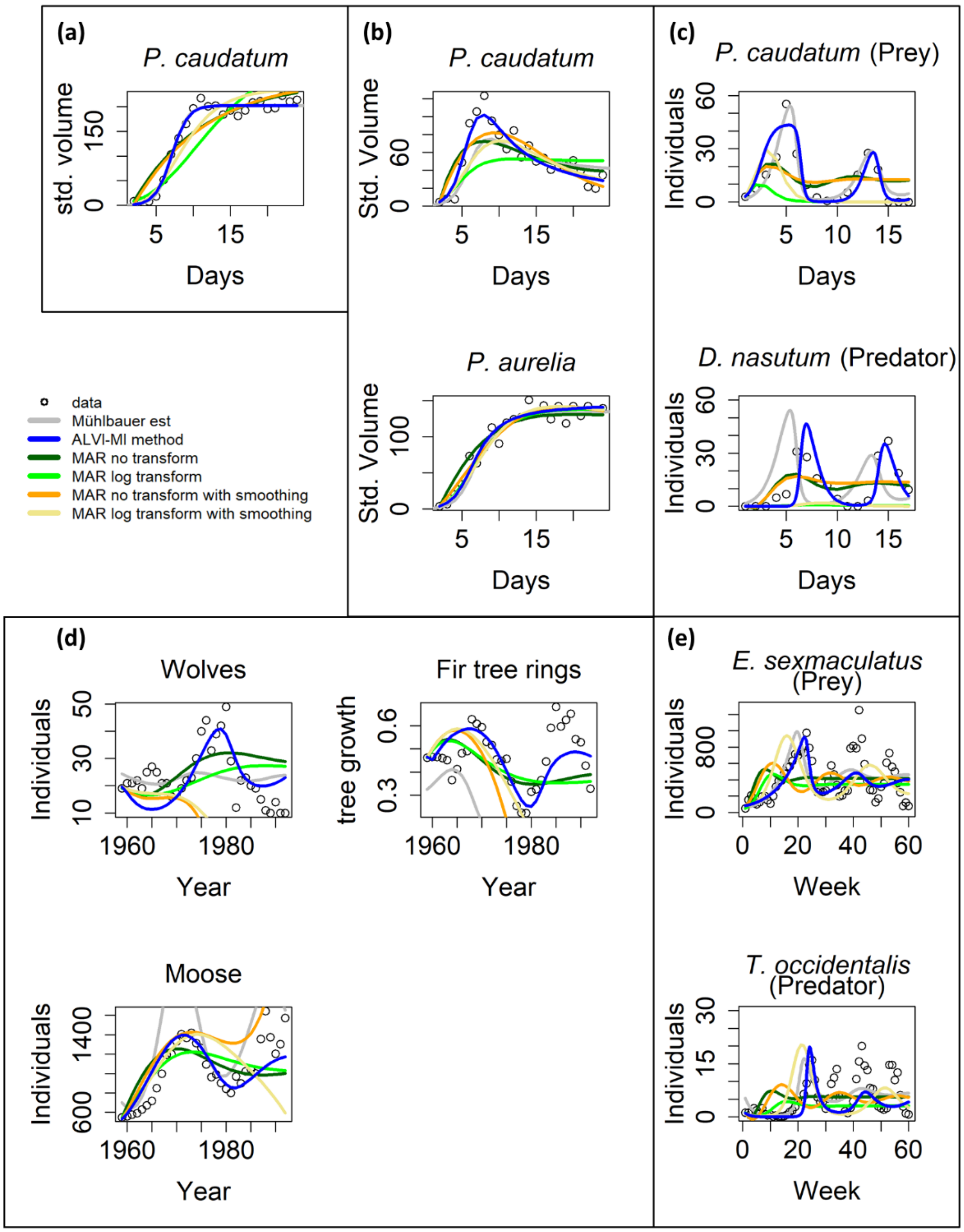

Figure 3: Model inferences associated with Gause's data (Gause, 1934). Circles show observations, gray lines are the estimates from Mühlbauer *et al.* (Mühlbauer et al., 2020). ALVI-MI method estimates are presented as blue lines and MAR estimates as green, orange and yellow lines. See text and *Supplements* Tables S4.1 and S4.3 for further details.

For the case in Figure 3a, ALVI-MI yields the same results as found in (Mühlbauer et al., 2020). In contrast, the MAR estimates are poor, with a very high estimate for the noise (Table S4.3), especially if one does not use log-abundances; this problem occurs in all cases presented in Figure 3. The data in Figure 3a are close to a logistic function, similar to X_4 in the previous noisy dataset, where MAR also did not perform well.

Figure 3b shows data from a competition experiment between *Paramecium caudatum* and *Paramecium aurelia* that were co-cultured. Estimates for *P. aurelia* are similar for all methods but ALVI-MI exhibits clear superiority for *P. caudatum*.

The data in Figure 3c are complicated. Mühlbauer and colleagues noted that aditional quantities of bacteria were introduced to avoid species extinction. Furthermore, many datapoints in this dataset are zero, which causes problems for the parameter estimators. As a remedy, we changed the zeros to 10^{-5}, but our initial estimates still produced poor fits. However, if we use the estimated trajectories from Mühlbauer *et al.* as "data," quasi as a diagnostic measure, ALVI-MI captures the parameters that reproduce the fit of Mühlbauer *et al.*. This finding suggests that the initial poor fit is not a problem of LV adequacy. Instead, we hypothesize that the problem was caused by insufficient datapoints or almost-linear dependence, which affects the matrix inversion. To test this hypothesis, we used the first splines as data to create a second set of splines that has more datapoints to create the subsample to be used on ALVI-MI. We were able to achieve the presented fit, which is still somewhat inferior to the one by Mühlbauer *et al.,* but a considerable improvement over our initial fits.

When calculating splines for this dataset, it is difficult to choose degrees of freedom that capture both maxima. High degrees of freedom capture the global maxima but overshoot the local maxima. Low degrees of freedom capture the local but undershoot the global maxima. We suspect this to be the cause of ALVI's initial poor performance. Still, ALVI yields better fits than MAR.

The data in Figure 3d are also complicated, in this case due to two aspects. First, they show a stark difference in absolute numbers, with the abundance values for moose being several magnitudes higher than the numbers of tree rings. As a potential remedy, we normalized the fitting error for each dependent variable by dividing it by its mean to balance the SSE. The result is shown in Figure 3d. The LV models perform better than MAR, and MAR with log-abundances produces a better noise estimate than with the untransformed data.

The second issue is the fact that, around 1980, the wolves were exposed to a disease introduced by dogs that caused a precipitous drop in the population between 1981 and 1982 (Park Service, 2021). Typical mathematical models are not equipped to simulate such a black swan event, and the totality of results from the various methods suggests that neither LV nor MAR may be good models for this system, because none of the fits, by Mühlbauer *et al.*, ALVI, and MAR, are entirely satisfactory. Nonetheless, our ALVI results present a decent fit for moose and fir tree rings. To improve the fit to the wolf data, we divided the data into two groups, from 1959 to 1980 and from 1983 to the end of the series and estimated parameters for the two intervals. The results are presented in Figure S7 in orange lines. The fit is greatly improved, although still not perfect.

Figure 3e describes yet another complicated example. According to the inference, the ALVI-MI estimates fit the first peak well but the oscillations die down, in contrast to the data. Estimates from Mühlbauer *et al.* produce even poorer estimates, suggesting that the data may not be compliant with the LV structure. As in the previous example, MAR models do not capture the dynamics, although MAR with log-abundances produces good noise estimates. Surprisingly, MAR with smoothing presented very poor fits to these data.

We repeated the analysis using ALVI-LR instead of ALVI-MI. The results were by and large similar and slightly inferior; they are shown in *Supplements* Figure S6 and Table S4.2.

One should note that Mühlbauer *et al.* used a steepest-descent method, while our method did not. Therefore, our results could possibly be further improved by adding a refinement cycle of steepest-descent optimization. The main problem of these algorithms, getting stuck in local minima, would presumably not be an issue, since the ALVI results are already close to the optimum.

3.3.2. Published MAR inferences

Here we use two datasets presented in the MAR inference package MARSS. The first dataset, "gray whales," consists of 24 annual abundance estimates of eastern North Pacific gray whales during recovery from intensive commercial whaling prior to 1900 (Gerber, Demaster, & Kareiva, 1999). It is thus to be expected that the whales are initially far from the carrying capacity of the system. The second case consists of data for wolf and moose populations on Isle Royale in Lake Superior between 1960 to 2011; this dataset was used by Holmes and colleagues (Holmes et al., 2020) to demonstrate usage of the MARSS R package.

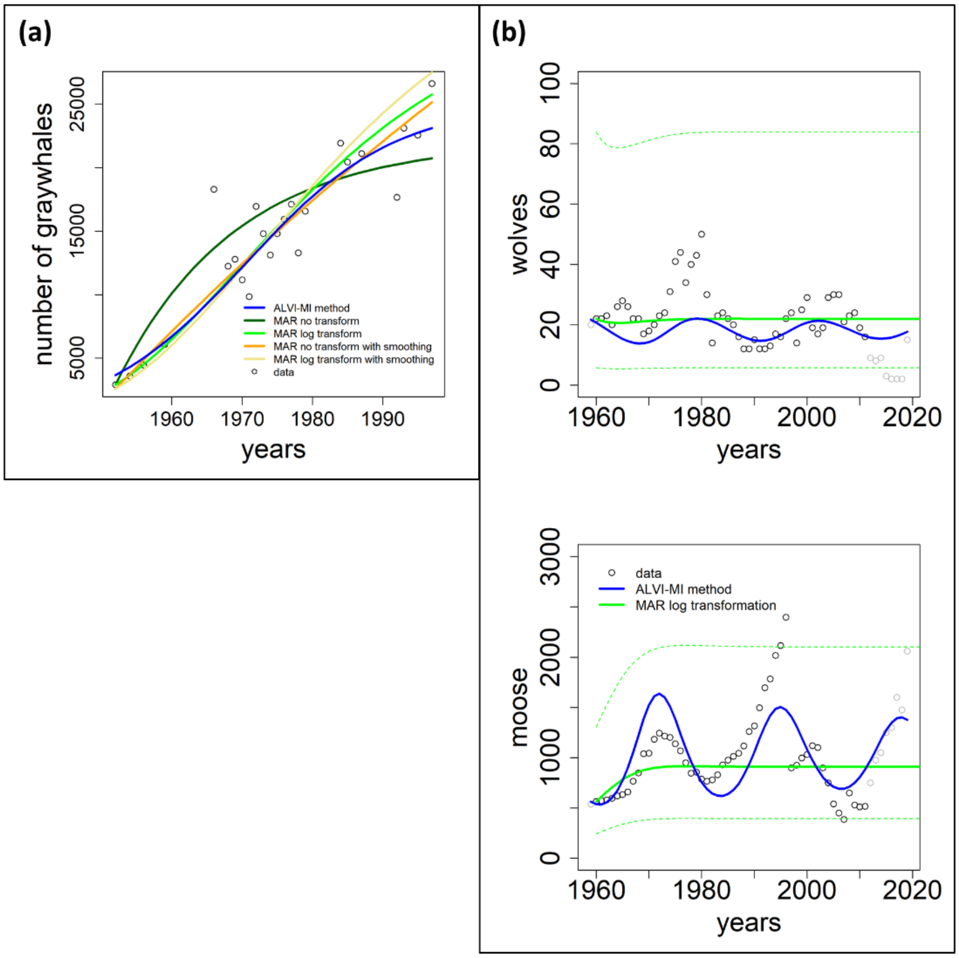

Figure 4: Two datasets of wildlife observations. Column a: Abundance data of gray whales (Gerber et al., 1999). The plot shows results from ALVI-MI in blue; MAR estimates are displayed with green, orange and yellow lines. Column b: Wolves and moose on Isle Royale (Vucetich, 2021). The original data used for parameter estimation are displayed with black circles, data not used by the estimation processes are shown in gray, ALVI-MI results are in blue, MAR estimates using log-abundances are displayed with green lines. The dashed lines indicate confidence intervals for the MAR estimates. Values of the estimates can be seen in Table S6.

Figure 4a show fits to the gray whale data (Gerber *et al.*, 1999). ALVI-MI noticeably outperforms MAR, even though the data came from a MAR demonstration. In particular, the MAR results suggest that the whales are close to regaining their carrying capacity, which seems to contradict the trend in the data. The SSEs can be seen in Table 1. It is unclear why the MAR method without transformation does not perform better. As it stands, the estimates are inadequate (with the highest SSE) and have a very high variance for the error. An LV model with one variable is a logistic function, and the LV fit represents initial quasi-exponential growth that starts to slow down after a while. This behavior nicely reflects the fact that the whales were recovering from very small numbers due to overfishing but are apparently still much below the carrying capacity.

Figure 4b returns to the Isle Royale dataset from Vucetich (Vucetich, 2021), which we already used in the context of examples from the collection of Mühlbauer and colleagues (Mühlbauer et al., 2020); *cf*. Figure 3. Holmes *et al.* (Holmes et al., 2020) used only the data of wolves and moose for a MAR analysis but extended them over a longer time horizon. Specifically, eight datapoints were added since the former usage of this dataset by Holmes and colleagues, from 2012 to 2020 (gray symbols in Figure 4b).

The results of the MAR model are identical with those published in (Holmes et al., 2020), with the same log transformation and z-scoring of the data, and the same parameter values were inferred. The result consists of acceptable estimates, although we found a slightly better fit without the z-scoring. Still, for a direct comparison, we opted to present the example exactly as Holmes *et al.* did. Interestingly, these fits miss all oscillatory behavior seen in the data. The ALVI results do show oscillations but clearly suffer from the disruption in the wolf population in 1981 and 1982, as discussed before.

Because we used in this example only MAR with log transformation, we display the confidence intervals for the MAR model as dashed green lines. Very few datapoints are outside the confidence intervals.

3.4. Comparative summary of the performance of LV and MAR in the presented examples

Inspection of Table 1 renders is evident that ALVI clearly performs better than MAR. In a few cases, the ALVI-LR solution gives a better SSE than ALVI-MI, but the difference between the two is not substantial. ALVI-LR appears to be superior when the data are noise-free.

Table 1 – Sum of squared errors (SSE) of data fits for all experiments with ALVI-LR, ALVI-MI and four variants of the MAR methods. We also include SSEs for the estimates obtained by Mühlbauer *et al.* (2020) for LV data presented in Figure 3. Bold values identify the lowest SSE score for each example. Examples used in the Wilcoxson rank test are marked with asterisks.

	Shown in	ALVI-LR	ALVI-MI	MAR	MAR logTrans	MAR with smoothing	MAR with log and smoothing	Mühlbauer *et al.*	Test
Noisy LV dataset	Fig. 1a	9.009	**4.362**	37.31	53.31	7.364	8.260		*
Replicate LV dataset	Fig. 1b	11.41	**2.953**	6.247	5.439	13.87	42.83		*
Noisy MAR dataset	Fig. 2a	2,727	1,142	**908.3**	37,447	1,191	1,604		*
Replicate MAR dataset	Fig. 2b	2,518	1,462	933.1	**177.967**	1,773	1,482		*
SynthData1	Fig. S5a	**3.29E-07**	9.04E-07	10.49	4.626				
SynthData2	Fig. S5b	8.68E-06	**8.57E-06**	3.029	5.876				
SynthData3	Fig. S5c	**0.002**	0.018	5.111	4.378				
SynthData4	Fig. S5d	**5.65E-04**	2.10E-02	2.47E+04	3.99E+35				
SynthData5	Fig. S5e	**7.048**	18.94	16.59	15.70				
SynthData6	Fig. S5f	71.27	**28.36**	7,379,825	174.2				
Mühlbauer et al. 1	Fig. 3a	2,588	**2,516**	18,160	51,738	17,877	16,399	3271	*
Mühlbauer et al. 2	Fig. 3b	6,204	**4,781**	13,016	22,162	9,293	12,447	40604	*
Mühlbauer et al. 3	Fig. 3c	24,183	**2,191**	4,619	10,146	4,780	8,795	578.1	*
Mühlbauer et al. 4	Fig. 3d	17,700,169	**1,118,350**	2,199,174	17,77,559	9,904,281	3,973,876	7934136	*
Mühlbauer et al. 5	Fig. 3e	12,114,811	**2,251,804**	4,245,588	4,450,871	5,596,187	4,554,089	2893764	*
Holmes et al. 1	Fig. 4a	168,134,153	153,703,251	217,478,452	166,186,993	**143,728,190**	212,424,910		*
Holmes et al. 2	Fig. 4b	32,326,913	**5,556,585**	10,267,681	10,947,294	11,136,306	14,342,449		*

We used a one-sided Wilcoxson rank test to see if the differences in performance are significant. The results and alternative hypotheses for these tests are presented in Table 2.

Table 2 - Test results of one-sided Wilcoxson rank.

Null hypothesis H_0:	Alternative hypothesis H_1:	*p*-value
SSE values of ALVI-MI are equal or higher than corresponding MAR values	SSE values of ALVI-MI are less than corresponding MAR values	**0.0093**
SSE values of ALVI-MI are equal or higher than corresponding MAR values for log transformed variables	SSE values of ALVI-MI are less than corresponding MAR values for log transformed variables	**0.0024**
SSE values of ALVI-MI are equal or higher than corresponding MAR values for smoothed data	SSE values of ALVI-MI are less than corresponding MAR values for smoothed data	**0.0269**
SSE values of ALVI-MI are equal or higher than corresponding MAR values for log transformed variables and smoothed data	SSE values of ALVI-MI are less than corresponding MAR values for log transformed variables and smoothed data	**0.0005**
SSE values of the ALVI-MI are equal or higher than SSE values obtained with the ALVI-LR	SSE values of ALVI-MI are less than SSE values obtained with the ALVI-LR	**0.0005**
SSE values of MAR with data smoothing are equal or higher than MAR values without	SSE values of MAR with data smoothing are less than MAR values without	0.7676
SSE values of MAR with log transformation and data smoothing are equal or higher than those for MAR with log transformation values	SSE values of MAR with log transformation and data smoothing are less than those for MAR with log transformation values	0.7935

The data supports that the ALVI-MI method produces smaller SSE's than the other methods considered. Also, in the last two tests, the data do not show evidence that data smoothing reduces the SSE's in MAR.

Comparing the results ALVI-LR and ALVI-MI with respect to the absolute value of the difference between true and estimated parameters, we obtained mixed results (Table 3). Indeed, a one-sided Wilcoxson rank test with the alternative hypothesis that the absolute errors in parameter values associated with ALVI-LR were smaller than those associated with ALVI-MI did not yield a significant *p*-value (0.2783).

Table 3 – Absolute differences between true and estimated parameters for ALVI-LR and ALVI-MI. Bold font indicates the lower difference in each case. A statistical test did not reject the null hypothesis of no difference between the results of the two methods.

	ALVI-LR	ALVI-MI
Noisy Data 5%	**1.97538**	2.68019
Replicate Data 5%	**0.24117**	0.32537
Noisy Data 20%	**1.35692**	46.60082
Replicate Data 20%	0.8835	**0.66838**
Synthetic Data 1	**0.00021**	0.00038
Synthetic Data 2	0.20832	**0.15534**
Synthetic Data 3	1.06975	**0.0982**
Synthetic Data 4	**0.19183**	0.60795
Synthetic Data 5	0.82403	**0.36212**
Synthetic Data 6	**0.18794**	0.97794

Comparing the values in Tables 1 and 3 for noisy and replicate datasets, the latter presented smaller values. However, using the one-sided Wilcoxson rank test for the values in Table 1 with the alternative hypothesis—that the SSE values for the replicate dataset were smaller than those for the noisy datasets—did not yield a significant *p*-value (0.2734). For the values in Table 3, the test produced a *p*-value (0.0625) smaller than 0.1, suggesting that time series data are better than clustered data for parameter estimation in LV using ALVI.

4. Discussion

We have compared LV and MAR models using, as parameter estimation strategies, a recently introduced ALVI method for LV models (Voit et al., 2021) and the established MARSS method for MAR models (Holmes et al., 2012). Summary Table 1 renders it evident that ALVI usually outperforms MARSS, with often substantially lower SSE values, and that LV models in the vast majority of cases provide better representations than MAR models. Furthermore, Certain *et al.* (Certain et al., 2018) prescribed the length of the data series as at least 5 times greater than the number of nonzero interaction elements in order to recover interaction signs correctly. A caveat is that we presented the MAR model equations without noise, thereby ignoring an important part of these models that characterizes the stochastic structure of the data.

ODEs and MAR models are derived from different philosophies and comparing them fairly is not straightforward. Here we compared the two approaches from a point of view of someone who is more interested in capturing the dynamics of a phenomenon, which poses an immediate disadvantage for MAR models, because they were created for phenomena with random noise and for characterizing the structure of this noise. Consequently, we found much of the dynamics quantified as noise in the estimates. Thus, an overarching conclusion is that the two approaches are different tools that are adequate in different situations. MAR models are well suited for simulations with variables presenting low abundances and investigations where the quantification of noise is relevant. By contrast, LV models, and ODE models in general, are better suited to capture the dynamics of a phenomenon and for cases where the dependent variables have high abundances and a high signal-to-noise ratio. Nonetheless, if the characterization of noise is of interest, one might subtract the LV fit from the raw data and then assessing the remainder. Another advantage of LV models is that ALVI permits *a priori* tests for the adequacy of the LV structure for a given dataset (Voit et al., 2021).

Because the LV structure is continuous, we can evaluate it at any point or choose any interval between the points in the numerical solution. By contrast, MAR does not truly reveal a time resolution higher than its intrinsic interval between solution points. However, Holmes *et al.* (Holmes et al., 2012) demonstrated with the MARSS R function that it is feasible to interpolate any number of missing values between the known datapoints, and that this method can be used to decrease the time unit for stepping forward. While this step does not make the MAR model as densely time-resolved as an ODE model, it mitigates the apparent granularity disadvantage considerably.

ALVI allows a choice between linear regression and matrix inversion. The former is simpler, because it uses all points available, and faster due to the fact that no data sample needs to be chosen. In most cases tested, it also produces good fits and estimates. However, the latter usually produces slightly better results and works well even in cases where the ALVI-LR solution fails (Table 1). It also offers a natural approach to inferring whole ensembles of well-fitting model parameterizations.

Results obtained with MARSS or with ALVI-LR are rather robust if the data are noisy, whereas solutions with ALVI-MI may be sensitive to small alterations in the data. As an example, consider the synthetic MAR data presented in Figure 2, where we added noise as a normally distributed variable with mean zero and standard deviation of 0.2 of the dependent variable mean. For comparison, consider now an alternative sample (Figure S8) obtained by applying the same procedure, but with a different seed for noise creation. The alternative dataset is almost indistinguishable from the original dataset in Figure 2, but using the same point sample determined for the original dataset, ALVI-MI produces different parameter values. This means that if we calculate a new set of splines, we should also search for a new point sample. The conclusion is that, although the inferred fits are similarly good, the parameter values associated with the best fit for a noisy point sample may not be optimal for another noisy sample, which may not be surprising. In fact, we showed in a different example with noise that the inferred parameter values yielded a better SSE than even the true values (Section 3.1). The argument may also be turned around into a positive feature: Different noisy datasets or subsamples of these datasets can easily be used to create natural ensembles of models that characterize the underlying data in a robust manner and yield additional insights into the variability of the model parameters.

The MARSS software makes modeling with MAR models easy, although not entirely automatic, as many options must be tested to find the one that returns the best fit in each case. For example, one must decide whether to use estimated initial conditions or the initial datapoints and which variables should have the same noise level. By contrast, the ALVI method for LV models is novel (Voit et al., 2021), and while all steps are straightforward and code is available on GitHub [https://github.com/LBSA-VoitLab/Comparison-Between-LV-and-MAR-Models-of-Ecological-Interaction-Systems], no formally published software currently exists that encompasses all these steps in a streamlined manner. As a new tool, ALVI offers several avenues for further refinement. One important component is optimal data smoothing with splines, which requires the determination of a suitable number of degrees of freedom and may also employ weights for different variables within a dataset.

A comparison of MARSS results with or without log transformation of the dependent variable abundances did not yield clear results. If the MAR models are to be viewed as a multispecies competition models with Gompertz density dependence (Certain et al., 2018), the log transformation is required (*Supplements* Section 1.3). While inferences for LV models usually benefit from smoothing, the same is not true for MAR model, where smoothing in some cases, but certainly not always, led to improved data fits (Table 2).

MARSS uses a steepest decent optimization step, which ALVI presently does not. Although ALVI already performs better than MARSS (Table 1), it might be possible to improve its results even further by adding a refinement step based on steepest-descent optimization. Steepest-descent methods tend to get trapped in local minima if the initial guesses are poor, but ALVI would not likely encounter this problem, as the solutions are already very good and could be used directly as initial guesses for the refinement step.

Estimation and inference methods typically do not scale well. ALVI bucks this trend, at least to some degree, as both the smoothing and estimation of slopes occur one equation at a time. Thus, instead of scaling quadratically, the inference problem scales linearly. The ultimate matrix inversion or linear regression is essentially the same for all realistically sized models. Thus, the only time-consuming step within ALVI-MI is the choice of datapoints. An exhaustive test for all combinations grows quickly in complexity, but it is always possible to opt for a random search. The resulting solution is not necessarily the best possible, but can still provide an excellent fit or at least a valuable starting point for a steepest-decent refinement optimization. Importantly, many random solutions can also be collated to establish an ensemble of well-fitting models, which in most cases yields more insight than a single optimized solution.

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6. Author Contributions

D.V.O., J.D.D., and E.O.V. conceived this project, performed the literature review, created the synthetic data examples and wrote of the manuscript. D.V.O. produced the code required for the study. All authors reviewed and edited the manuscript.

7. Data Accessibility

The R code for running the experiments is available on GitHub:

https://github.com/LBSA-VoitLab/Comparison-Between-LV-and-MAR-Models-of-Ecological-Interaction-Systems

8. Additional Information

Competing financial interests

The authors declare no competing interests.

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SUPPLEMENTS

Comparison Between Lotka-Volterra and Multivariate Autoregressive Models of Ecological Interaction Systems

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1. Materials and Methods

1.1. Lotka-Volterra models

For a single variable, Lotka-Volterra (LV) models (Eq. [1] in the main text) reduce to the well-known logistic growth law

$$\frac{dX_{i,t}}{dt} = a_i X_{i,t} - b_{ii} X_{i,t}^2, \qquad [\text{ S1 }]$$

where the ratio a_i/b_{ii} is called the "carrying capacity" of the system, which corresponds to the non-trivial steady state. If time-dependent environmental inputs are to be considered, one may add terms $\gamma_i X_i U_t$, where U_t is an element of a vector of these inputs and the coefficients γ_i are weights that quantify the effects of the factors on species X_i (Stein et al., 2013; Dam *et al.*, 2016; Dam *et al.*, 2020). The index *t* is usually omitted, and the left-hand side is often written as $\dot{X}_i$.

The LV system is a *canonical* model in the sense that its mathematical structure is immutable and scalable to any dimension (Voit, 2000). Such a canonical model may serve as a template to construct models of different systems that reasonably satisfy the following assumptions:

- encounters between and within species are representable by mass action kinetics;

- the environment does not change during the process, unless environmental variables are explicitly formulated as described above;
- the parameter values do not change during an experiment;
- the species respond to one another instantaneously;
- for very small population sizes, interactions are negligible and the rate of change (growth) of each population is initially proportional to its size, resulting in initial exponential growth;
- adaptations of species are absent or negligible.

Although the model structure and these assumptions might appear to be unduly rigid, LV models are extremely rich in the repertoire of their possible responses. In fact, the LV structure was shown to be capable of modeling any type of differentiable nonlinearities, including different kinds of oscillations and chaos (Vano et al., 2006), if sufficiently many auxiliary variables are permitted, some of which have mathematical, but no real biological meaning (Voit & Savageau, 1986; Peschel & Mende, 1986; Savageau & Voit, 1987). At the same time, the LV structure has severe limitations. For example, it is not well suited for metabolic pathway systems, because a simple conversion of a substrate X_1 into a product X_2 would require X_2 to appear in its own synthesis term, although the generation of X_2 in truth depends only on X_1 and possibly some modulators (see (Voit, 2013) for this and other limitations).

LV models were initially used to describe the dynamics of predator and prey populations or of populations that compete for the same resources, but the same equations have also been used in entirely different contexts and fields, including physics (Nambu, 1986; Hacinliyan, Kusbeyzi, & Aybar, 2010), pollution assessment (Haas, 1981), economy (Zhou & Chen, 2006; Gandolfo, 2008), manufacturing (Chiang, 2012), and sales (Hung, Chiu, Huang, & Wu, 2017).

Beyond the fact that LV models can be formulated very easily, another significant advantage over other systems of nonlinear ODEs is the fact that LV models can be parameterized with linear regression methods if time series data are available (Voit & Chou, 2010). As an intriguing alternative, the linearity also permits us to select variable and slope values at *n*+1 time points and to obtain parameter inferences by solving a set of linear algebraic equations (see below). It is furthermore possible to estimate parameter values from sufficiently many profiles of species that initially coexist and ultimately survive under comparable conditions (Voit et al., 2021).

1.2. Estimation of LV Parameters Based on Slopes of Time Courses

This section explains in detail an approach to parameter estimation that uses the Algebraic Lotka-Volterra Inference (ALVI) method. For a detailed explanation of the ALVI method itself please see (Voit et al., 2021).

1.2.1. Smoothing

Even though one might consider smoothing a conceptually separate issue from the actual parameter inference, the two are so closely intertwined in our analysis that it appears useful to discuss smoothing options. The goal is two-fold. First, it is beneficial to reduce or even remove noise from the raw data, and second, this smoothing greatly aids the determination of slopes of the experimental time courses (see later).

A smoothed representation of a dataset implicitly integrates information that is not in the data. This implicit integration step is not entirely unbiased and requires prudent judgment, because it must answer the following questions, often without true knowledge of the system: Are the deviations between the data and the smoothing function due to (stochastic) noise or are they part of the true signal? For instance, are they the trace of true oscillations? Also, if very few data points deviate much more than all others from the smoothing function, are they true peaks or valleys or are they statistical outliers? It is difficult to answer these questions objectively, but two features of the data are of great benefit: First, if the variation in noise amplitude is much smaller than the range of signal values (high signal-to-noise-ratio), the distinction between signal and noise is relatively straightforward. Second, if the data come in replicates, they may support or refute the potential of true oscillations or peaks at certain time points in the data. Even if only one dataset is available, the biologist familiar with the phenomenon at hand usually has developed an expectation regarding signal and noise, and if there is no biological rationale for expecting oscillations or strong deviations from some simple trend, the smoothing strategies are flexible enough to allow the integration of the biologist's knowledge and expectations. The result of the smoothing process therefore is a synthesis of all relevant information, constrained by external knowledge and reasonable expectations. Of course, it is also feasible to create alternative models with different thresholds between signal and noise and to analyze them side by side.

Independent of the options and intricacies of obtaining smoothed time courses of all variables, it is well known that the process of estimating slopes from data is more strongly affected by noise than the data themselves (Knowles & Renka, 2014). Expressed differently, if the noise is left unchecked, its effect on the estimated values of the slopes tends be higher than its effect on the values of the variables.

We explored a number of methods for smoothing the time course data and keeping the noise in check (Eilers, 2003; Vilela et al., 2007; Batista Júnior & Pires, 2014), cognizant of the fact that empirical raw data alone do not provide enough information of what is noise and what is relevant signal in the dynamics of the phenomenon under study.

One of the simplest approaches is the *three-point method*, where the slope at time point t_k is taken as the average of the slopes at time points t_{k-1} and t_{k+1} (Burden, Faires, & Burden, 1993; Voit & Almeida, 2003).

More sophisticated methods were reviewed in (Cleveland & Grosse, 1991; Eilers & Marx, 1996; Batista Júnior & Pires, 2014). For long, dense time series, moving average and collocation methods with or without roughness penalty (Ramsay et al., 2007) are often very effective. However, they tend to be unsuited for biological time series data because the measurements are usually quite sparse and obtained over a relatively short time horizon.

Smoothing splines and *local regression* methods like LOESS (locally estimated scatterplot smoothing) and LOWESS (locally weighted scatterplot smoothing) turned out to be particularly useful. A detailed description of these methods can be found in (Cleveland, 1981).

In a nutshell, splines are piecewise polynomial functions that: pass through all sample points, are continuous and have first and second derivatives that are continuous at junction points between adjacent intervals. In a smoothing spline, the first condition is substituted by a least-squares fit that is balanced with an additional criterion that penalizes splines with high second derivative values, which indicate local roughness (Cleveland, 1979; Garcia, 2010; Loader, 2012).

LOESS and LOWESS algorithms use locally-weighted polynomial regression. LOWESS is used for univariate smoothing and consists of computing a series of local linear regressions, with each local regression restricted to a window of x-values. Smoothness is achieved by using overlapping windows and by gradually down-weighing points in each regression according to their distance from the anchor point of the window. LOESS is for fitting a smooth surface to multivariate data and it is a generalization of LOWESS in that locally weighted univariate regressions are simply replaced by locally weighted multiple regressions. While LOESS is more versatile, LOWESS is faster and sometimes succeeds when LOESS fails (Cleveland, 1979; Cleveland & Devlin, 1988; Smyth, 2020). Locally-weighted polynomial regression methods have 'span' and splines have 'degrees of freedom,' which are parameters that control the degree of smoothing.

The main result of smoothing with splines is a reduction or even removal of what is believed to be noise in the data. The slope at each point can be computed directly from the smoothing spline, which after all is an explicit function. This step of slope determination offers two options: it allows us to estimate slopes only for the measured data points or to sample the smoothing function for any number of other points, which yields a larger set of numerical values for variables and slopes (Voit & Almeida, 2004).

If we select many points from the smoothing spline, we overcome the problem of data scarcity that is inherent in many datasets. In fact, sampling from the smoothing spline allows the subsequent parameter inference method to access a larger amount of information and thereby to mitigate noise amplification.

1.2.2. Conversion of ODEs into systems of algebraic equations

If data are available as time series, it is mathematically feasible and beneficial to estimate slopes (for instance, from smoothing splines) and to convert the inference problem from one based on ODEs into one exclusively using algebraic functions (Voit & Savageau, 1982a, 1982b; Varah, 1982; Torres & Voit, 2002; Voit et al., 2005).

Suppose the growth and interaction parameters of an LV system are to be estimated from time series data of the dependent variables X_i. The smoothing of these data facilitates the estimation of slopes $S_k(X_i)$ of all variables at a set of time points t_k, k = 1, …, K. These time points may or may not correspond to the measured data. In fact, the smoothing permits the computation of slopes at arbitrarily many time points within the observation interval. However many slopes are computed, they correspond to derivatives of the spline of X_i at the given time points. Substituting numerical values of all variables and slopes from the smoothing splines into Eq. (1) yields a system of $n \times K$ linear algebraic equations containing all system parameters:

$$S_{i,t} = a_i X_{i,t} + \sum_{j=1}^{n} b_{ij} X_{i,t} X_{j,t},\ \ i = 1, \dots, n \qquad [\ S2\ ]$$

If environmental inputs $\gamma_i X_{i,t} U_t$ are to be considered as well, they are added to the equations and either substituted with numerical values, if known, or estimated with the parameters a_i and b_{ij}.

A caveat of this conversion of ODEs into algebraic equation is a possible time warp (see end of chapter 5 of (Voit, 2017)). The reason is that time is explicitly eliminated from the procedure. Nonetheless, the estimates usually provide good results, or at least good initial guesses for other optimization approaches such as traditional gradient methods.

Suppose the dependent variables are not zero within the dataset obtained from smoothing. If so, we can divide both sides of the *K* equations for X_i in expression [S2] by the value of the dependent variable at the appropriate time point. This step is not mandatory but linearizes the equations. The case of variables with values of zero is typically not very interesting or can be handled by eliminating the variable or parts of the time series.

1.2.3. Parameter inference

Once all differentials are replaced with estimated slopes, the inference of parameter values from LV-models offers two options: because the system of algebraic equations is linear, we may optimize its parameter values through simple multivariate linear regression (ALVI-LR), where we may use data points or iterate the regression with subsets of points, which naturally leads to an ensemble of well-fitting models.

An interesting alternative is to use just *n*+1 of the data points and slopes, if *n* is the number of variables, which results in a system of linear equations that can be solved with simple algebraic methods (ALVI-MI).

Choosing different data points naturally creates ensembles of solutions. These can be further analyzed, for instance, with respect to model robustness and identifiability. They can also be used to determine to what degree the LV format is adequate for the available data (Voit et al., 2021).

1.2.4. Example of parameter estimation with ALVI

To explain the parameter estimation procedure with ALVI, we use the sparse noisy dataset presented in *Supplements* Section 2 and also in Table S1.2. First, we smooth the data with a spline or LOESS. For this example, we use 5, 8, 11 and 5DF-splines for X_1, X_2, X_3 and X_4 respectively and compute the first derivative of the splines to estimate the slopes. At this point we discard the data and only use the spline values. We may use the original data, especially if we think they characterize the studied phenomenon well, but using the spline usually produces better results in the case of noisy data.

As an example, consider the first differential equation and the first datapoint, at t = 0:

$$\frac{dX_1}{dt}(0) = a_1X_1(0) + b_{11}X_1(0)X_1(0) + b_{12}X_1(0)X_2(0) + b_{13}X_1(0)X_3(0) + b_{14}X_1(0)X_4(0)$$

We substitute numerical values for the slope and for all variables on the system equations,

time	Slope_X_1	X_1	X_2	X_3	X_4
0	0.0353	1.229	0.492	1.787	0.0367

which yields

$$0.0353 = a_1 \times (1.229\ ) + b_{11} \times (1.229)^2 + b_{12} \times (1.229\ ) \times (0.492)$$
$$+ b_{13} \times (1.229) \times (1.787) + b_{14} \times (1.229\ ) \times (0.0367).$$

We may divide the equation by the numerical value of the dependent variable, but this step is not mandatory.

$$\frac{0.0353}{1.229} = a_1 + b_{11} \times (1.229\ ) + b_{12} \times (0.492) + b_{13} \times (1.787) + b_{14} \times (0.0367)$$

The same steps are performed for every equation and every chosen time point. The result is a system of linear equations with as many equations as chosen time points; each equation has n+1 unknown parameters, where n corresponds to the number of dependent variables.

Now we have two options: We may use linear regression (ALVI-LR) or matrix inversion (ALVI-MI). ALVI-LR uses every equation and every chosen time point and performs linear regression to produce estimates for the parameters. For the alternative, ALVI-MI, we choose a sample of data points that, when combined with the equations, generates a number of equations equal to the number of parameters to be estimated. If these equations are linearly independent, the system is solvable and the solution is unique, allowing us to obtain estimates for the parameters by simple matrix inversion.

1.3. Multivariate Autoregressive (MAR) models

Multivariate Autoregressive (MAR) models are discrete recursive models. Their format is shown in eqn. 2 and 3 of the main text and conveys that the state of the system at time t+1 depends on the state at t and possibly on environmental or stochastic input. As an alternative to this modeling structure with "memory 1," it is possible to extend MAR models to depend also on states farther in the past, such as X_{t-1}, X_{t-2}, and X_{t-3}, in addition to X_t. However, the commonly used models depend only on the immediately prior state and are sometimes called MAR(1). Here, we only consider MAR(1) models and refer to them simply as MAR models.

MAR models can be interpreted in two distinct ways. In generic mathematical terms, MAR models are stochastic, linear approximations of nonlinear dynamic systems that evolve over time in the vicinity of a fixpoint (steady state). According to this interpretation (Holmes et al., 2013), X_t is a vector of the realization of random variables at time t. Noise captures natural variations in environmental conditions and is modeled by a multivariate normal distribution with mean zero and variance-covariance matrix $\boldsymbol{\delta}$. If stochasticity is omitted, MAR models are quite similar to LV models close to the steady state (see *Supplements* Section 1.5).

One may also interpret MAR models in an ecological context, where they can be viewed as multispecies competition models with Gompertz density dependence and an instantaneous growth rate that decreases linearly over time as the population sizes increase (Ives, 1995; Certain, Barraquand, & Gårdmark, 2018). In this context, X_t is a vector of the log-abundances of dependent variables at time t.

MAR models may be augmented with state variables that simulate the observation process and these models are called Multivariate Autoregressive(1) State-Space (MARSS) (Holmes et al., 2012; Certain et al., 2018); we will not analyze these for the sake of simplicity. For the comparisons in this study, we are not considering the influence of environmental variables, so the $\boldsymbol{\gamma u}_t$ term will be omitted henceforth.

It is considered an advantage in ecology if models explicitly take the influence of environmental factors into account (for details, see (Certain et al., 2018) (Hytti et al., 2006)), which is the case for MAR. The availability of estimation software like MARSS (Holmes et al., 2012, 2020) has greatly increased the appeal of MAR models.

1.4. MARSS

MARSS is a software package for analyzing MAR models with or without log transformation of the dependent variables. Its use requires several steps.

1 – Specify key MARSS settings:

B = "unconstrained"	Matrix with all elements potentially different
U = "unequal"	Vector with all elements potentially different
Q = "diagonal and unequal"	Matrix where all elements are zero except the main diagonal, where the elements have real values
Z = "identity"	Identity matrix
A = "zero"	All elements zero
R = "zero"	All elements zero
x0 =	Initial values of the time series

A and **R** correspond to the "observation variables," which simulate the observation process of the system variables. For our comparisons, these are set to zero because observation variables are not considered.

2 – In the MARSS function, the data must be formatted with variables in rows and observations in columns. If the data points are not equally distributed in time, they must be augmented by "NA" to force the interval between any two consecutive data entries to be of the same length. This is necessary to ensure the correct time structure of the data for the estimator.

3 – With this regularization, MARSS finds estimates for **B**, **U** and **Z**, that correspond to α, β and δ in eqn 3 of the main text.

If MARSS does not converge, it is advisable to increase the max number of iterations. This step solves the problem but is different from the suggestion offered by Holmes and colleagues, namely, that the model assumptions should be checked (see p. 57 in (Holmes et al., 2020)).

Our setup is exactly equal to that used by Holmes *et al.* (Holmes et al., 2012, 2020) for the Isle Royale dataset, which the authors used to exemplify the inference of species interaction parameters with and without covariates. Some of the illustration examples were modeled differently in the literature but for purpose of comparisons with LV models, this model structure was used. For example, the 'gray whales' dataset was modeled by Holmes and colleagues with β, the species interaction matrix, set to zero, whereas **R**, the matrix that captures the noise from the observational process, was estimated from the data. Because we are interested in the interactions between species, we do not focus on observational noise, and Holmes' original setup was replaced with the one discussed above.

1.5. Structural Similarities between Modeling Formats

The two modeling formats appear to be very different mathematically. Nonetheless, they can be compared in terms of their mathematical representations and also with respect to practical considerations. These comparisons demonstrate that the two models can actually behave quite similarly if the community of populations operates relatively close to a stable steady state. By contrast, if this assumption is violated, the two models often show strongly diverging results, as the linearity of the MAR model can deviate considerably from the nonlinearities of the LV model.

Purely considered on mathematical grounds, MAR is defined recursively in eqn 2 and 3 of the main text. By omitting environmental variables, we directly obtain

$$X_{i,t+1} = \alpha_i + \sum_{j=1}^{n} \beta_{ij} X_{j,t} + w_{i,t};\ i = 1,2,\dots,n;\quad w_{i,n} \sim N(0,\delta_i), \qquad [\text{S3}]$$

which can be interpreted as a multispecies competition model with Gompertz density dependence, if the dependent variables represent logarithmic abundancies (Certain et al., 2018).

Suppose that the MAR model indeed uses log-abundances. To explain similarities between the MAR and LV formats, we rewrite this multispecies log-abundance model equivalently in Cartesian form, which yields the following:

For $i = 1,2,\ldots, n;\;\; w_{i,n} \sim N(0,d_i)$:

$$\begin{aligned}
&\ln(X_{i,t+1}) = \alpha_i + \sum_{j=1}^{n} \beta_{ij} \ln(X_{j,t}) + w_{i,n} \\
&\Leftrightarrow X_{i,t+1} = e^{\left(\alpha_i + \sum_{j=1}^{n} \beta_{ij} \ln(X_{j,t}) + w_{i,n}\right)} \\
&\Leftrightarrow X_{i,t+1} = e^{\alpha_i} e^{\left(\sum_{j=1}^{n} \ln\left((X_{j,t})^{\beta_{ij}}\right)\right)} e^{w_{i,n}} \\
&\Leftrightarrow X_{i,t+1} = e^{\alpha_i} \prod_{j=1}^{n} e^{\left(\ln\left((X_{j,t})^{\beta_{ij}}\right)\right)} e^{w_{i,n}} \\
&\Leftrightarrow X_{i,t+1} = e^{\alpha_i} \prod_{j=1}^{n} (X_{j,t})^{\beta_{ij}} e^{w_{i,n}} \quad [\text{ S4 }]
\end{aligned}$$

In this form, MAR is similar to a discrete multivariate power-law function.

The similarity of this result to the LV model can be seen if we use Euler's method for determining the numerical solution. Euler's method is an approximation of more sophisticated methods and its simplicity makes it preferable for the comparisons between time series and ODEs.

Formulating the typical Euler step for the LV model transforms the ODE into a series of discrete steps of the type

$$X_{i,t+h} = X_{i,t} + h * \left.\frac{dX_i}{dt}\right|_{X_i = X_{i,t}} = X_{i,t} + h * X_{i,t}\left(a_i + \sum_{j=1}^{n} b_{ij} X_{j,t}\right), \quad i = 1,2,\ldots, n, \qquad [\text{ S5 }]$$

where *h* is the step size of Euler's method and dX_i/dt is the left-hand side of the differential equations in eqn 1, evaluated at time *t.*

A comparison of eqn [S4] and [S5] suggests that the MAR and LV models seem to be very different. Whereas the LV model captures nonlinear dynamic behaviors without variable transformations, the MAR model uses linearity in log space. Nonetheless, there are similarities between the two formats. To see these, we compare eqn [S3] and [S5] instead of [S4] and [S5].

Furthermore, we suppose that the dynamics is near the steady state of the differential equations, so that $X_{i,t+1} - X_{i,t} \approx 0$ for any given t. Using this approximate equality in eqn [S3], we obtain

$$X_{i,t+1} - X_{i,t} \approx 0$$

$$\Leftrightarrow \alpha_i + \sum_{j=1}^{n} \beta_{ij} X_{j,t} + w_{i,t} - X_{i,t} \approx 0;\ i = 1,2,\ldots, n;\quad w_{i,n} \sim N(0,\delta_i). \qquad [\text{ S6 }]$$

Using this approximate equality in format [S5] for LV yields, for $i = 1,2,\ldots, n$:

$$X_{i,t+h} - X_{i,t} \approx 0$$

$$\Leftrightarrow X_{i,t} + h * X_{i,t}\left(a_i + \sum_{j=1}^{n} b_{ij} X_{j,t}\right) - X_{i,t} \approx 0$$

$$\Leftrightarrow a_i + \sum_{j=1}^{n} b_{ij} X_{j,t} \approx 0$$

$$\Leftrightarrow a_i + \sum_{j=1}^{n} \tilde{b}_{ij} X_{j,t} - X_{i,t} \approx 0 \qquad [\text{ S7 }]$$

Here $\tilde{b}_{ij}$ equals b_{ij} for all $i \neq j$ and $b_{ij} + 1$ lor $i = j$.

If we disregard the Gaussian noise, w_{ij}, in the MAR model, the two sets of near-steady-state eqn [S6] and [S7] are the same. They are both linear, although the dynamic LV model itself is non-linear. Thus, if $\alpha_i = a_i$, $\beta_{ij} = b_{ij}$ for all $i \neq j$ and $\beta_{ij} = b_{ij} + 1$ for $i = j$, the MAR and LV models are mathematically equivalent at the steady state and similar close to it. As long as the nonlinearity are close to linear or close to power-law functions, MAR without or with log-transformation, respectively, may be expected to lead to acceptable fits.

2. Case study 1: Synthetic LV data

As a representative example, we use the four-variable LV system

$$\frac{dX_{i,t}}{dt} = a_i X_{i,t} + b_{i1} X_{i,t} X_{1,t} + b_{i2} X_{i,t} X_{2,t} + b_{i3} X_{i,t} X_{3,t} + b_{i4} X_{i,t} X_{4,t}, \quad i = 1, \dots, 4 \qquad [\text{ S8 }]$$

The parameters are presented in Figure S1. For a first analysis, we use this system to create one set of synthetic time courses, consisting of 100 time points, which is presented in Table S1. The dynamics is shown in Figures 1 and S1 as circles.

If we use these noise-free data, the inferences are close to perfect with respect to the trajectories and parameter values (Figure S9).

To mimic a more realistic scenario, we created a noisy dataset, visualized in Figure S1a, which was constructed by randomly choosing forty of the one hundred original datapoints obtained from the synthetic system and adding to the chosen points a normal random variable with mean 0 and a standard deviation of 20% of the mean of each variable. This *noisy dataset* is shown in Table S1.2.

A second realistic dataset (Figure S1b) was constructed by first choosing eleven points from the data that characterize the dynamic (including extremes values). Next, each of the chosen points was multiplied by a random normal variable with mean 1 and standard deviation of 0.2. This process was iterated to create five replicates per chosen point. This *replicate dataset* is shown in Table S1.3.

Variable X_4 was designed as a (decoupled) logistic function. It is unaffected by the other variables and does not affect them either. It was included to explore to what degree the methods to be tested can detect this detachment.

The smoothing and slope estimation steps followed directly the procedures described in *Supplements* Section 1.2. The first derivative of the smoothing function was used for estimates for the slopes.

To infer numerical values for the parameters of a given equation, we have the choice between linear regression (ALVI-LR) and algebraic matrix inversion (ALVI-MI). For ALVI-MI, we choose points from the sample and use the corresponding slope estimates to create a system of equations with the same number of equations and unknowns. As we have 4 variables and 20 parameters, we need 20 independent equations and thus 5 time points. For each time point we obtain the value for each of the 4 dependent variables and use these to populate the equations.

As an illustration for the noisy dataset, we choose 5, 8, 11 and 5DF-splines and time points t = 8, 13, 17, 19 and 79 for the noisy dataset. For the replicate dataset, we use 5, 6, 8 and 8DF-splines, and the ALVI-MI solution was calculated with spline points at times 11, 18, 26, 33 and 60. The time point selection for the ALVI-MI solution can be automated using a random or exhaustive search of the possibilities.

The noisy dataset (Figures 1a, S1a, S3a and S4a) is representative of a study where each time point sample corresponds to a single observation taken when it is possible or convenient. By contrast, the replicate dataset (Figures 1b, S1b, S3b and S4b) simulates a series of experimental replicates where the observations were conducted multiple times, but at fewer time points, which the researchers suspect would contain valuable information.

As an illustration of how the smoothing techniques work, we used splines and LOESS with different degrees of smoothing. The results for variable X_1 are shown in Figure S2. Choosing the optimal degree of smoothing is not a trivial matter. Too much smoothing ignores important details in the variable dynamics, while too little incorporates noise. In the programing language R, the function “loess.as” allows the calculation of the optimum value for the spam, which controls the smoothing. The user still must decide the degree of the polynomials to be used and choose from two criteria for automatic smoothing parameter selection: a bias-corrected Akaike information criterion (AICC) and generalized cross-validation (GCV). This choice is not always leading to the optimal solution, but it should be used to challenge our assumptions.

Figure S3 presents the same treatment as presented in Figure 1 but for datasets with 5% noise. It is clear and not surprising that the models produce better quality fits when the signal-do-noise ratio is higher.

2.1.1. Application of ALVI to synthetic data

An alternative to using the algebraic parameter inference method with matrix inversion (ALVI-MI) is the linear regression method (ALVI-LR); fits for 20% noise are shown in Figure S4. As in ALVI-MI, the parameter values are close to the true values and the fit is acceptable. However, the dynamics of the system is slightly different. One reason is that the dynamic solutions are sometimes quite sensitive to the chosen initial values. As a remedy, it is often beneficial to initiate the solution somewhere inside the overall time interval, typically close to the midpoints of the variable ranges, and solve forward and backward.

ALVI also works for more complicated dynamics, as can be seen in Figure S5. Here we are interested in finding out if the methods can recover the dynamics, which in some cases turns out to be challenging for sparse data even without the introduction of noise. Thus, we used the synthetic data unaltered. Specifically, data for early time points (t = [1, 100]) were fitted and then extrapolated for a total time horizon of (t = [1, 500]). In these examples, ALVI-MI is used with 100DF-splines. It uses data samples with points corresponding to timepoints t = 5, 10, 20, 30 and 50 for all cases except for the chaotic oscillations where we used t = 4, 6, 10, 15 and 35. For each case, we also present the MAR estimates. Of course, one must recall that the original data were produced with LV models. While the MAR model extrapolations are not always satisfactory, it is nevertheless comforting that the inference method returns good results for the time interval used for data fitting.

ALVI-MI generally performed very well but did not adequately capture the deterministic chaos (chaos 1). For this case only, we obtained a better fit using ALVI-LR, which may not be surprising given the extremely sensitive nature of chaotic systems to noise. Apart from this situation, results with ALVI-LR are very similar to ALVI-MI results and will not be displayed.

In Figure S5b, the MAR model performed well when log-abundances were used. In the remaining cases, it failed to replicate the oscillations or these exploded by reaching amplitudes far bigger than in the dataset. One also notes early discrepancies between the initial points used to create the estimates and the MAR estimates.

3. Supplemental Figures

Figure S1

	Initial Conditions
X_1	1.2
X_2	0.3
X_3	2
X_4	0.001

	True Parameter Values
a_1	0.044
b_{11}	-0.08
b_{12}	0.02
b_{13}	0.08
b_{14}	0
a_1	0.216
b_{11}	-0.04
b_{12}	-0.08
b_{13}	0.04
b_{14}	0
a_2	0.116
b_{21}	-0.16
b_{22}	0.16
b_{23}	-0.08
b_{24}	0
a_4	0.2
b_{41}	0
b_{42}	0
b_{43}	0
b_{44}	-0.1

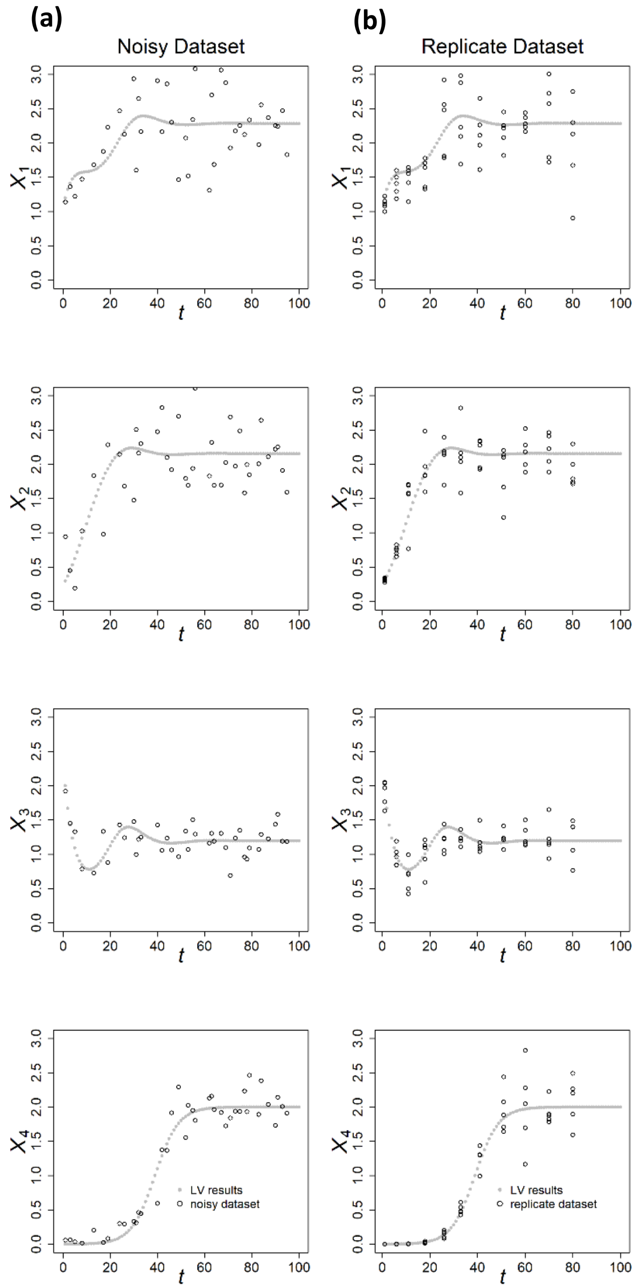


Figure S1: Time courses with superimposed noise. Initial conditions and parameter values for the synthetic LV example in equation S8 with four dependent variables. **Column a:** Noisy dataset – Based on 40 points from the synthetic data with added random normal noise with mean 0 and standard deviation equal to 20% of each variable mean. **Column b:** Replicate dataset – 11 points were chosen from the synthetic data and at each point five "observations" were created by multiplying the value of the variable by a random normal value of mean 1 and standard deviation of 0.2.

Figure S2

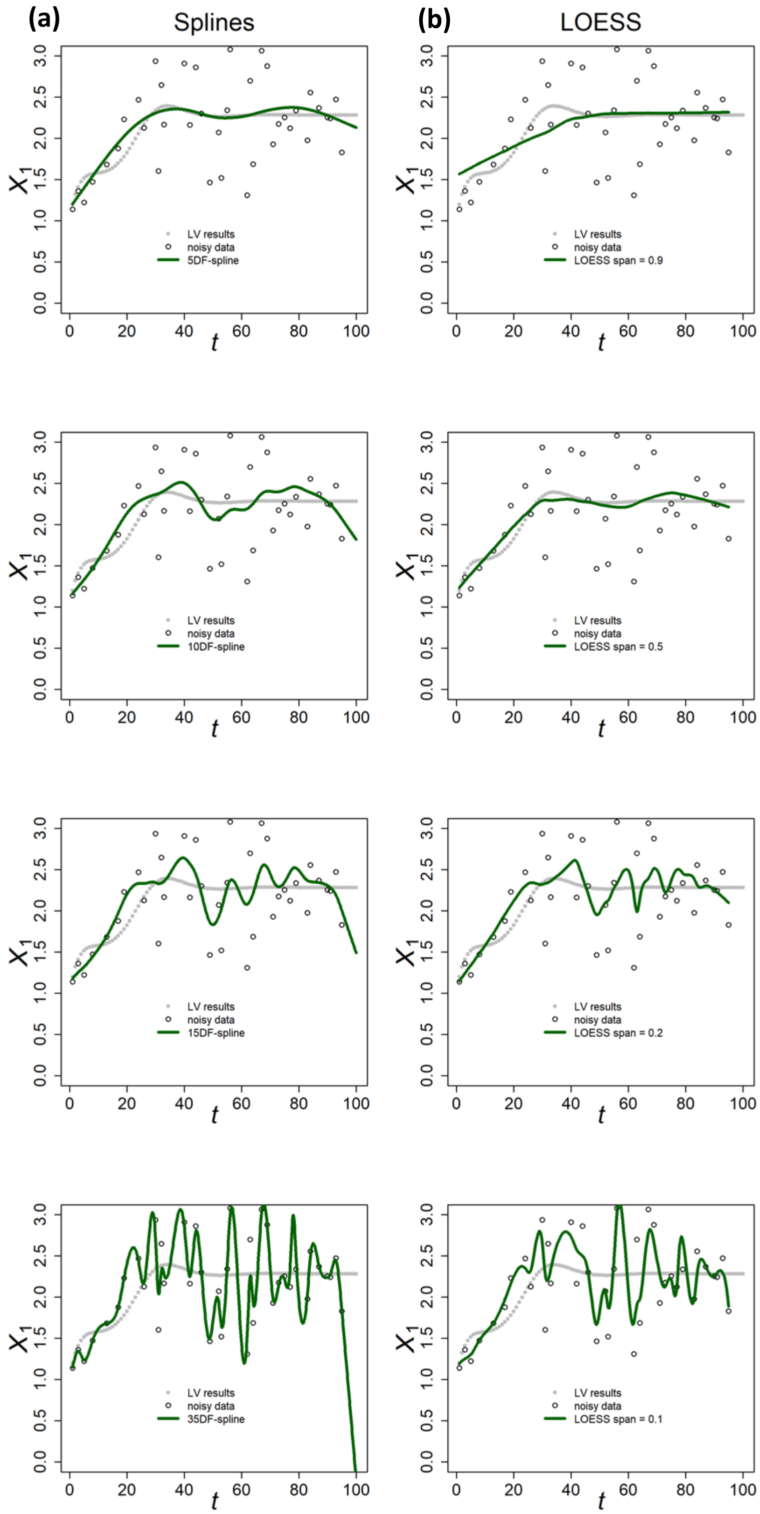


Figure S2: Smoothing noisy variable X_1. Column a: Splines with different degrees of freedom. **Column b:** LOESS with different span levels.

Figure S3

	Initial Conditions	Noisy Data	Replicate Data
X_1	1.2	1.25117	1.17824
X_2	0.3	0.25825	0.30397
X_3	2	1.69737	1.97235
X_4	0.001	0.02083	0.00104

	True Parameter Values	Noisy Data	Replicate Data
a_1	0.044	0.07373	0.03593
b_{11}	-0.08	-0.09759	-0.06540
b_{12}	0.02	0.02780	0.01935
b_{13}	0.08	0.07649	0.06434
b_{14}	0	-0.00149	-0.00401
a_1	0.216	0.24020	0.21072
b_{11}	-0.04	0.00429	-0.00647
b_{12}	-0.08	-0.08501	-0.09561
b_{13}	0.04	-0.04856	0.01263
b_{14}	0	-0.00323	-0.00423
a_2	0.116	0.10463	0.07192
b_{21}	-0.16	-0.13316	-0.16077
b_{22}	0.16	0.12651	0.16478
b_{23}	-0.08	-0.05638	-0.05221
b_{24}	0	-0.00441	0.00187
a_4	0.2	0.48906	0.19237
b_{41}	0	-0.79105	-0.00824
b_{42}	0	0.91565	0.00687
b_{43}	0	-0.30302	0.01005
b_{44}	-0.1	-0.15627	-0.09992

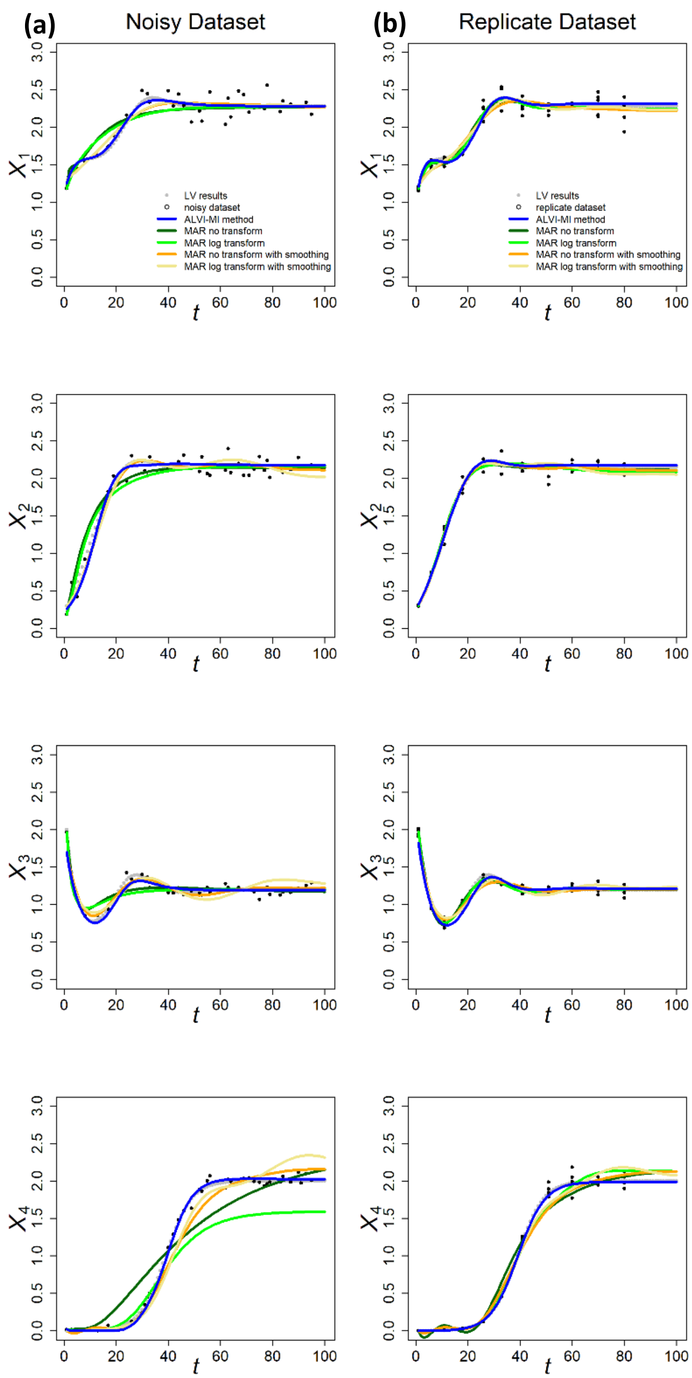


Figure S3: Results of ALVI-MI and MAR applied to the noisy and replicate datasets with 5% of noise. Column a: Noisy dataset. All variables were smoothed with 11DF-splines and the ALVI-MI solution was calculated with spline points at time points 8, 17, 30, 42 and 62. **Column b:** Replicate dataset. All variables were smoothed with an 8DF-spline and the ALVI-MI solution was calculated with spline points corresponding to time 6, 18, 26, 33 and 60. MAR estimates are presented in Tables S2.1 and S2.2.

Figure S4

	Initial Conditions	Noisy Data	Replicate Data
X_1	1.2	1.19177	1.13704
X_2	0.3	0.54552	0.33033
X_3	2	1.78728	1.75958
X_4	0.001	0.05701	0.00116

	True Parameter Values	Noisy Data	Replicate Data
a_1	0.044	0.05445	0.02433
b_{11}	-0.08	0.00671	-0.00738
b_{12}	0.02	-0.02130	-0.00173
b_{13}	0.08	-0.01411	0.01168
b_{14}	0	-0.00481	-0.01293
a_1	0.216	0.23293	0.21887
b_{11}	-0.04	0.00027	0.04438
b_{12}	-0.08	-0.01935	-0.11968
b_{13}	0.04	-0.14178	-0.04491
b_{14}	0	-0.01553	-0.00930
a_2	0.116	0.01081	-0.04261
b_{21}	-0.16	0.00380	-0.07696
b_{22}	0.16	0.04570	0.11963
b_{23}	-0.08	-0.08669	-0.02739
b_{24}	0	-0.00586	-0.00146
a_4	0.2	0.08891	0.16518
b_{41}	0	-0.02791	-0.02964
b_{42}	0	0.11969	0.02948
b_{43}	0	-0.11663	0.03522
b_{44}	-0.1	-0.06679	-0.10181

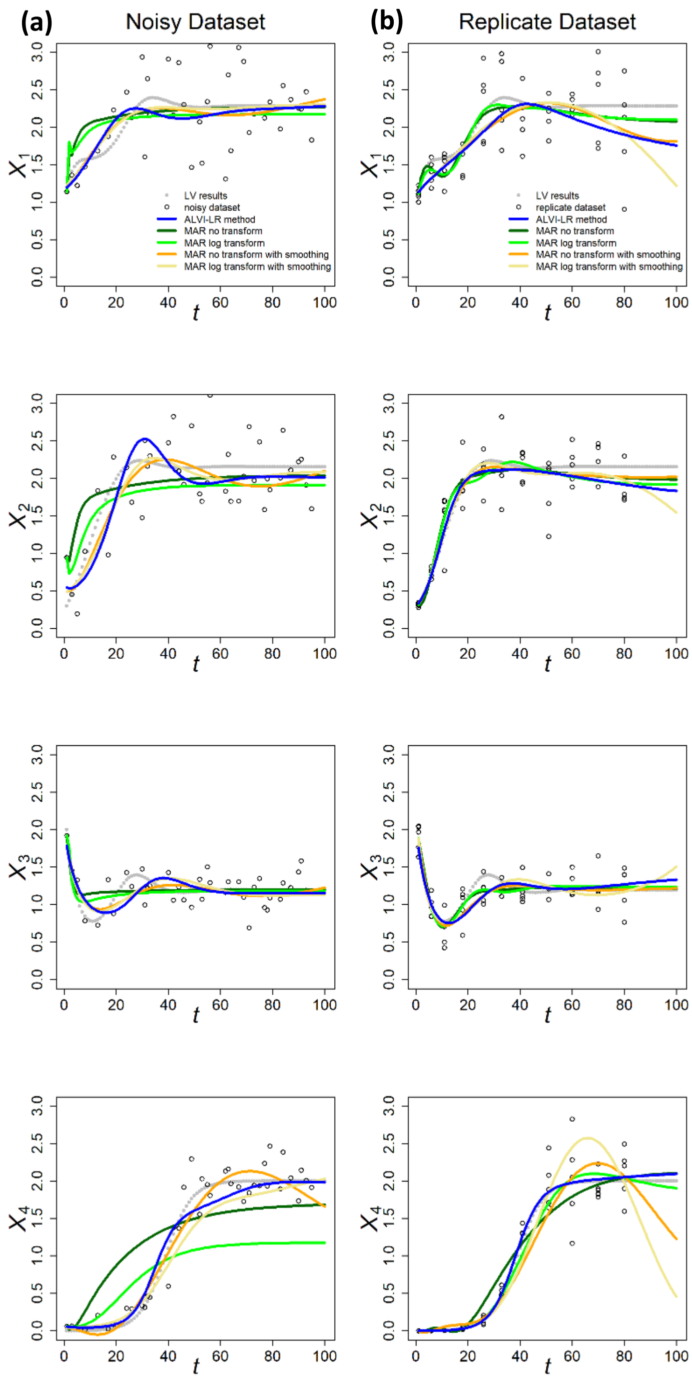


Figure S4: Results of ALVI-LR and MAR applied to the noisy and replicate datasets. Column a: Noisy dataset. Time courses of X_1, X_2, X_3 and X_4 were smoothed with 6, 11, 11 and 11DF-splines respectively. **Column b:** Replicate dataset. All variables were smoothed with 8DF-splines. MAR estimates are the same presented in Figure 1.

Figure S5

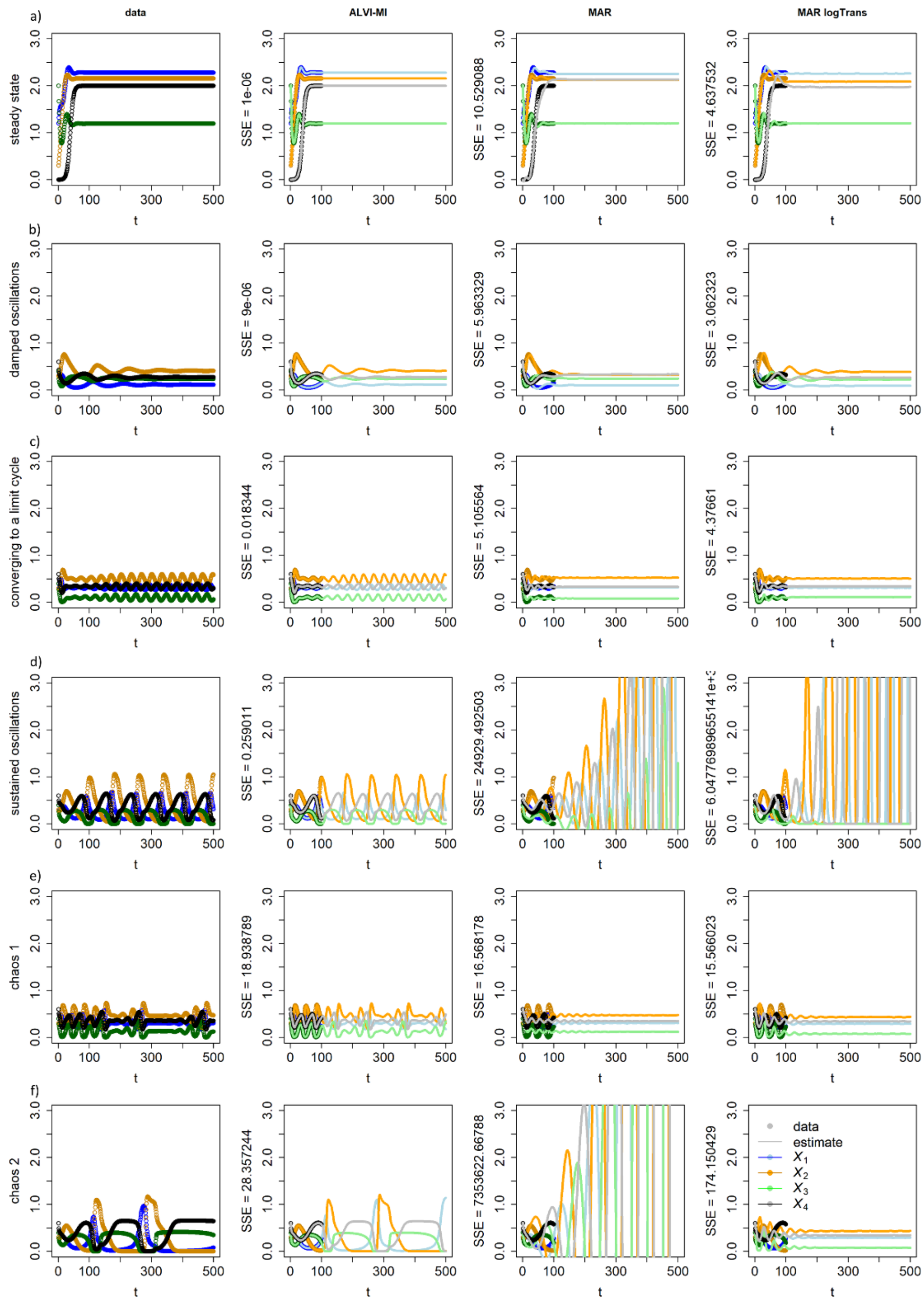


Figure S5 – Data and results of inferences with ALVI-MI and MAR methods for LV systems with different dynamics. Row a: Data converging to a stable steady state; **Row b:** Damped oscillations; **Row c:** Initially erratic oscillations converging to a limit cycle; **Row d:** Sustained oscillations; **Row e:** Deterministic chaos, example 1; **Row f:** Deterministic chaos, example 2. Data, ALVI-MI and MARSS estimates are presented in Table S3. The SSEs concerning the differences between the data and estimates for t = [1, 500] are presented as labels to the Y-axis. No smoothing preceded MAR because the data are noise free.

Figure S6

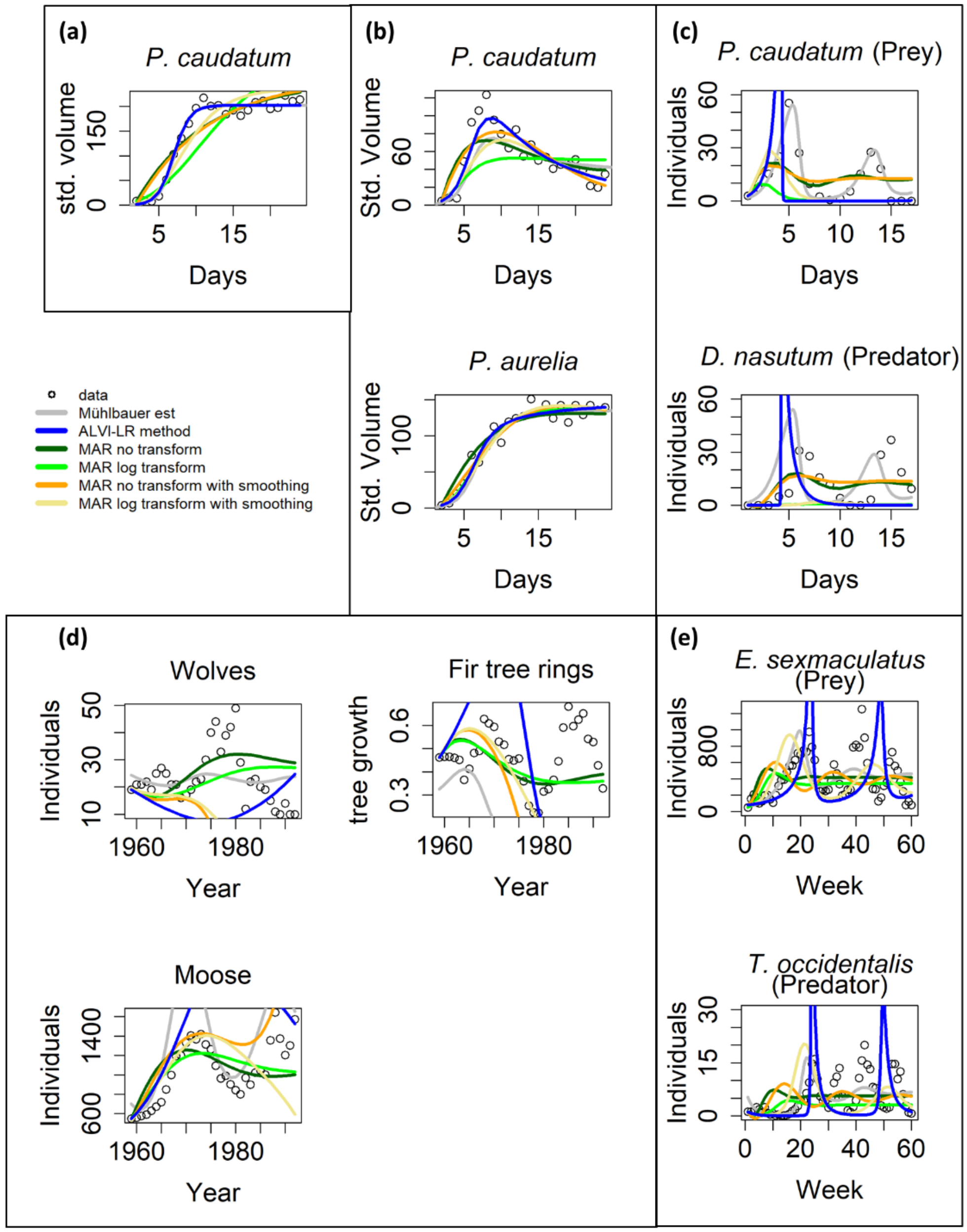


Figure S6 – Examples of experimental data analyzed with ALVI-LR and MAR. Black lines are estimates from Mühlbauer *et al.* (Mühlbauer et al., 2020). ALVI-LR estimates are represented as blue lines; corresponding parameter values can be seen in Table S4.2. MAR estimates are presented in green, orange and yellow. Parameter estimates are presented in Table S4.3. **a:** Standardized volume of *Paramecium caudatum* grown in monoculture (Gause, 1934). **b:** Standardized volume of *Paramecium caudatum* and *Paramecium aurelia* grown in co-culture (Gause, 1934). **c:** Predator-prey interactions between *Didinium nasutum* and *Paramecium caudatum* grown in mixture (Gause, 1934). **d:** Multi-trophic dynamics for wolves, moose, and fir tree rings on Isle Royale from 1960 to 1994 (McLaren & Peterson, 1994). **e:** Predator-prey interactions between *Eotetranychus sexmaculatus* and *Typhlodromus occidentalis* in a spatially structured experiment (Huffaker, Shea, & Herman, 1963).

Figure S7

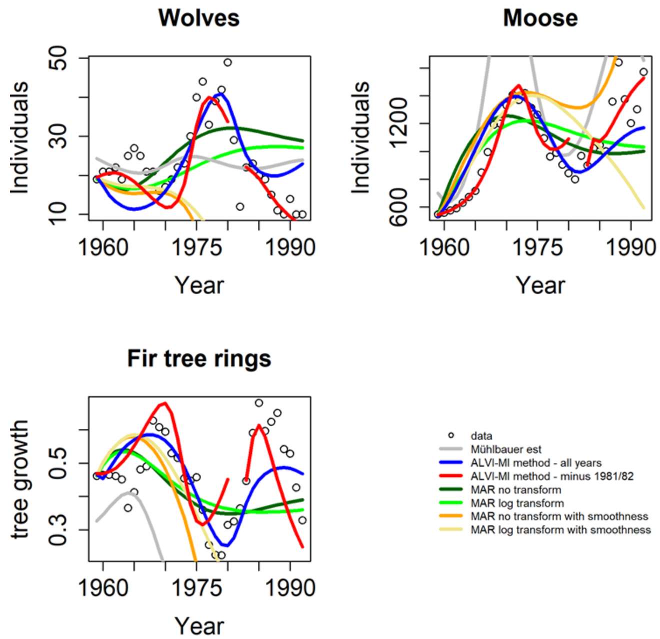
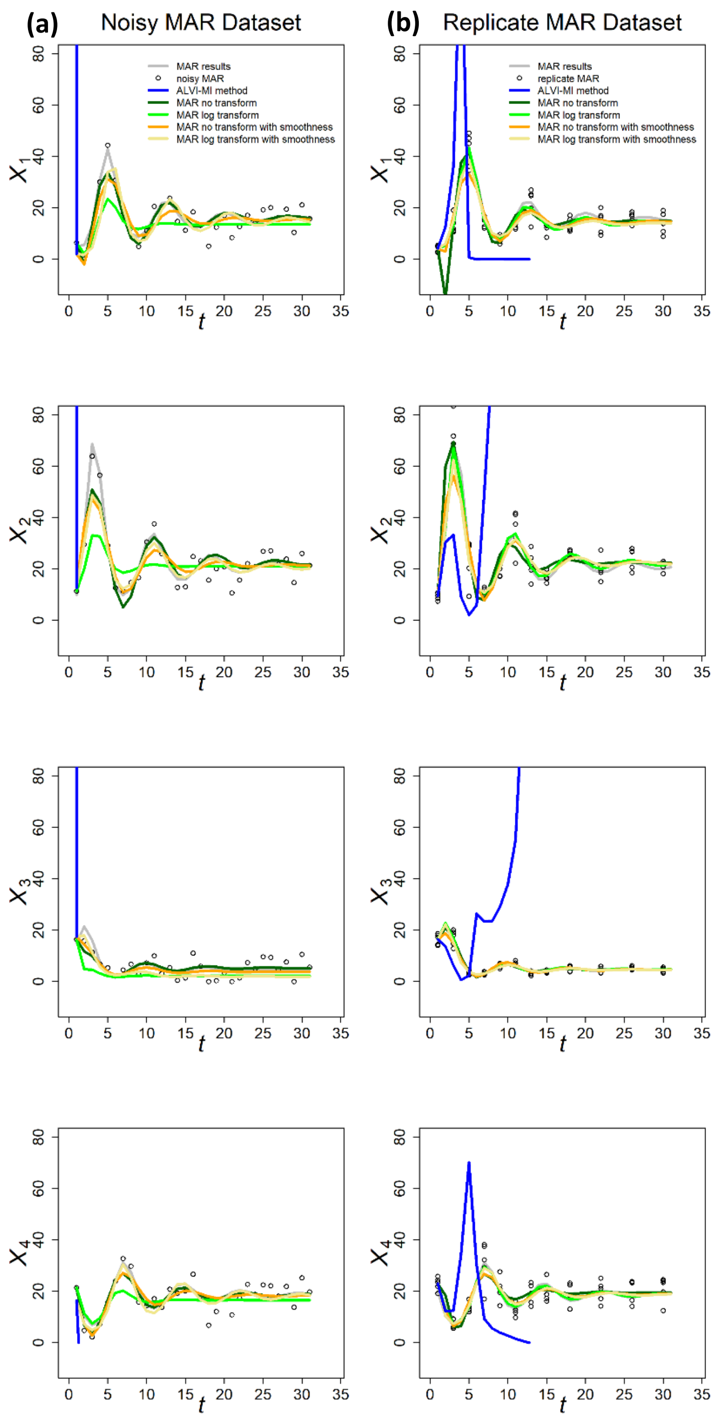


Figure S7 - Multi-trophic dynamics for wolves, moose, and fir trees on Isle Royale from 1960 to 1994, from McLaren & Peterson (1994) (McLaren & Peterson, 1994). This panel is very similar to Figure 2 d) but contains additional information. ALVI-MI estimates using all data are represented as blue lines. MAR estimates are presented in green, orange and yellow. Red lines correspond to the estimates using ALVI-MI for two intervals, from 1959 to 1980 and form 1983 until the end of the series. This split was tested because around 1980 the wolves were exposed to a disease that drastically reduced their numbers, an event that dynamic models do not capture outside piecewise operation. MAR estimates are the same as in Figure 3.

1005 **Figure S8**



1006

1007 **Figure S8: ALVI-MI and MAR applied to an alternative sample of the same data presented in Figure 4, but with**
1008 **slightly changed noise.** Although the differences in noise are visually almost undetectable, very different results for
1009 the ALVI-MI fit are obtained if the same sample of spline points is used. However, if a new sample of spline points is
1010 determined, the fits are almost indistinguishable (not shown). See Text for further explanations.

Figure S9

	Initial Conditions	ALVI-MI Estimates	ALVI-LR Estimates
X_1	1.2	1.2	1.2
X_2	0.3	0.3	0.3
X_3	2	2	2
X_4	0.001	0.001	0.001
	True Parameter values		
a_1	0.044	0.0440	0.0440
b_{11}	-0.08	-0.0800	-0.0800
b_{12}	0.02	0.0200	0.0200
b_{13}	0.08	0.0800	0.0800
b_{14}	0	0.0000	0.0000
a_1	0.216	0.2160	0.2160
b_{11}	-0.04	-0.0400	-0.0400
b_{12}	-0.08	-0.0800	-0.0800
b_{13}	0.04	0.0400	0.0400
b_{14}	0	0.0000	0.0000
a_2	0.116	0.1161	0.1161
b_{21}	-0.16	-0.1602	-0.1602
b_{22}	0.16	0.1601	0.1601
b_{23}	-0.08	-0.0799	-0.0799
b_{24}	0	0.0000	0.0000
a_4	0.2	0.2000	0.2000
b_{41}	0	-0.0003	-0.0003
b_{42}	0	0.0001	0.0001
b_{43}	0	0.0003	0.0003
b_{44}	-0.1	-0.0999	-0.0999

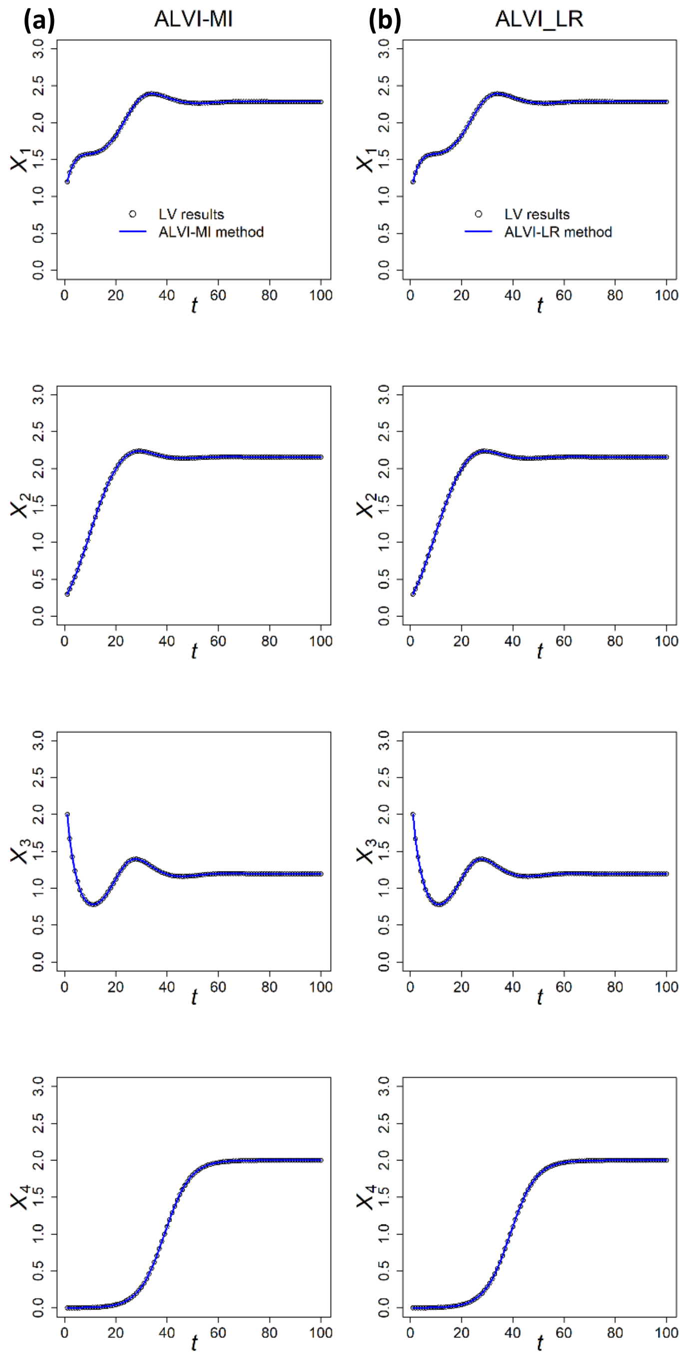


Figure S9: Estimates with alternative ALVI methods. Column a: ALVI-MI and **Column b:** ALVI-LR with original synthetic LV data. The fits are of high quality (ALVI-MI SSE = 1.162229e-05 and ALVI-LR SSE = 3.289283e-07) and the parameter estimates are very close to the true parameters.

4. Supplemental Tables

Table S1.1 – Synthetic LV data. The data were generated with an LV system with four dependent variables with parameter values presented in Figure S1.

t	X_1	X_2	X_3	X_4
0	1.20000	0.30000	2.00000	0.00100
1	1.32083	0.37078	1.67253	0.00122
2	1.41112	0.44848	1.42395	0.00149
3	1.47488	0.53265	1.23448	0.00182
4	1.51746	0.62275	1.09051	0.00222
5	1.54431	0.71810	0.98219	0.00272
6	1.56033	0.81785	0.90227	0.00332
7	1.56959	0.92096	0.84535	0.00405
8	1.57534	1.02621	0.80746	0.00494
9	1.58006	1.13229	0.78565	0.00603
10	1.58566	1.23781	0.77778	0.00737
11	1.59356	1.34144	0.78227	0.00899
12	1.60486	1.44195	0.79788	0.01097
13	1.62038	1.53828	0.82360	0.01338
14	1.64076	1.62958	0.85846	0.01632
15	1.66648	1.71521	0.90140	0.01990
16	1.69783	1.79474	0.95118	0.02425
17	1.73496	1.86789	1.00625	0.02954
18	1.77779	1.93449	1.06475	0.03596
19	1.82599	1.99445	1.12450	0.04375
20	1.87894	2.04769	1.18311	0.05317
21	1.93567	2.09416	1.23810	0.06457
22	1.99490	2.13382	1.28715	0.07830
23	2.05502	2.16666	1.32828	0.09482
24	2.11427	2.19279	1.36011	0.11461
25	2.17079	2.21241	1.38190	0.13823
26	2.22286	2.22591	1.39369	0.16628
27	2.26899	2.23381	1.39615	0.19943
28	2.30811	2.23680	1.39047	0.23832
29	2.33961	2.23566	1.37821	0.28360
30	2.36336	2.23123	1.36102	0.33585
31	2.37966	2.22437	1.34057	0.39550
32	2.38913	2.21586	1.31834	0.46281
33	2.39266	2.20642	1.29562	0.53773
34	2.39123	2.19665	1.27343	0.61988
35	2.38587	2.18704	1.25253	0.70850
36	2.37758	2.17796	1.23345	0.80243
37	2.36727	2.16968	1.21655	0.90013
38	2.35575	2.16237	1.20201	0.99980
39	2.34368	2.15612	1.18987	1.09947
40	2.33162	2.15098	1.18009	1.19718
41	2.32001	2.14691	1.17257	1.29113
42	2.30917	2.14387	1.16713	1.37978
43	2.29935	2.14177	1.16358	1.46196
44	2.29070	2.14052	1.16170	1.53691
45	2.28329	2.14001	1.16126	1.60424
46	2.27717	2.14013	1.16203	1.66392
47	2.27231	2.14076	1.16377	1.71620
48	2.26866	2.14180	1.16626	1.76151

49	2.26613	2.14313	1.16930	1.80043
50	2.26462	2.14467	1.17270	1.83359
51	2.26400	2.14632	1.17627	1.86167
52	2.26415	2.14801	1.17987	1.88531
53	2.26494	2.14968	1.18337	1.90511
54	2.26623	2.15128	1.18668	1.92164
55	2.26790	2.15275	1.18970	1.93538
56	2.26982	2.15407	1.19237	1.94679
57	2.27189	2.15523	1.19467	1.95622
58	2.27400	2.15620	1.19658	1.96401
59	2.27609	2.15698	1.19809	1.97044
60	2.27808	2.15759	1.19921	1.97573
61	2.27991	2.15802	1.19998	1.98009
62	2.28156	2.15829	1.20042	1.98367
63	2.28299	2.15842	1.20058	1.98661
64	2.28418	2.15843	1.20049	1.98902
65	2.28515	2.15833	1.20021	1.99100
66	2.28588	2.15816	1.19977	1.99263
67	2.28640	2.15792	1.19922	1.99396
68	2.28673	2.15764	1.19859	1.99505
69	2.28688	2.15733	1.19793	1.99595
70	2.28688	2.15702	1.19726	1.99668
71	2.28675	2.15671	1.19660	1.99728
72	2.28653	2.15641	1.19598	1.99777
73	2.28623	2.15613	1.19541	1.99818
74	2.28588	2.15588	1.19491	1.99851
75	2.28551	2.15566	1.19448	1.99878
76	2.28512	2.15547	1.19411	1.99900
77	2.28473	2.15532	1.19383	1.99918
78	2.28436	2.15521	1.19361	1.99933
79	2.28402	2.15512	1.19346	1.99945
80	2.28371	2.15507	1.19337	1.99955
81	2.28344	2.15504	1.19333	1.99963
82	2.28322	2.15503	1.19334	1.99970
83	2.28303	2.15505	1.19338	1.99975
84	2.28289	2.15508	1.19346	1.99980
85	2.28279	2.15512	1.19355	1.99983
86	2.28272	2.15517	1.19367	1.99986
87	2.28269	2.15522	1.19378	1.99989
88	2.28269	2.15528	1.19391	1.99991
89	2.28270	2.15533	1.19403	1.99993
90	2.28274	2.15539	1.19414	1.99994
91	2.28279	2.15544	1.19425	1.99995
92	2.28286	2.15549	1.19434	1.99996
93	2.28292	2.15553	1.19442	1.99997
94	2.28299	2.15556	1.19449	1.99997
95	2.28306	2.15559	1.19455	1.99998
96	2.28313	2.15562	1.19459	1.99998
97	2.28320	2.15563	1.19462	1.99998
98	2.28325	2.15564	1.19464	1.99999
99	2.28330	2.15565	1.19465	1.99999
100	2.28335	2.15565	1.19465	1.99999
101	2.28338	2.15565	1.19464	1.99999

Table S1.2 – Noisy LV dataset. From the synthetic data, generated with the LV system in Table S1.1, forty values were selected and random normal noise was added with mean 0 and standard deviation equal to 20% of each variable mean.

t	X_1	X_2	X_3	X_4
1	1.14111	0.94716	1.92175	0.06256
3	1.36364	0.45349	1.45431	0.06645
5	1.22283	0.19582	1.33123	0.03641
8	1.47489	1.02716	0.78493	0.01857
13	1.68296	1.83783	0.72635	0.20645
17	1.87602	0.98039	1.33307	0.02590
19	2.23270	2.28656	0.88182	0.08578
24	2.46929	2.14703	1.42853	0.30301
26	2.12740	1.68427	1.24384	0.29370
30	2.93876	1.47752	1.47634	0.33315
31	1.60470	2.50979	0.99567	0.31345
32	2.64561	2.16238	1.21792	0.46671
33	2.16612	2.30080	1.25219	0.44936
40	2.90825	2.47699	1.42807	0.59721
42	2.16482	2.82494	1.06154	1.37928
44	2.86258	2.10103	1.23401	1.37031
46	2.30199	1.92131	1.06248	1.91622
49	1.46650	2.70250	0.96520	2.29495
52	2.07311	1.79577	1.33918	1.55672
53	1.52180	1.69359	1.07106	2.03041
55	2.34261	1.94310	1.50543	1.95215
56	3.07809	3.11285	1.29445	1.80656
62	1.30983	1.83120	1.16429	2.13265
63	2.70020	2.32062	1.30813	2.15788
64	1.68571	1.69570	1.19108	1.96368
67	3.06508	1.69727	1.30761	1.92002
69	2.87653	2.02694	1.10203	1.72796
71	1.92870	2.69214	0.69211	1.84299
73	2.17466	1.97223	1.23306	1.94046
75	2.25649	2.48677	1.35097	1.93681
77	2.12334	1.58311	0.96197	2.23364
78	3.38719	1.99818	0.93052	1.93376
79	2.33980	1.85041	1.09020	2.46553
83	1.97877	2.01006	1.07131	1.89393
84	2.55545	2.64187	1.29245	2.38731
87	2.36884	2.11299	1.22538	2.03970
90	2.25285	2.22309	1.43866	1.73292
91	2.24325	2.25534	1.58509	2.14186
93	2.47453	1.91424	1.19010	2.00689
95	1.82853	1.59450	1.18877	1.91223

Table S1.3 – Replicate LV dataset. 11 points were selected from the synthetic data in Table S1.1. For each time point, five observations were created by multiplying the original value by a normal random variable with mean 1 and standard deviation 0.2.

t	X_1	X_2	X_3	X_4
1	1.079474	0.307892	1.968433	0.001177
1	1.228073	0.319118	1.767284	0.001143
1	1.001938	0.278408	2.035955	0.001019
1	1.151608	0.34439	2.049352	0.000994
1	1.106675	0.330651	1.634474	0.001462
6	1.409001	0.827832	1.033651	0.003136
6	1.292779	0.655128	0.840712	0.002841
6	1.186731	0.753583	0.964293	0.003671
6	1.501709	0.702128	0.846646	0.002595
6	1.600803	0.778034	1.191477	0.003243
11	1.553429	1.585188	0.501395	0.008283
11	1.420026	1.565142	0.721249	0.009309
11	1.599542	0.772725	0.708241	0.004804
11	1.642382	1.707548	0.424371	0.00881
11	1.142047	1.689577	0.992655	0.00613
18	1.644046	1.84217	0.929999	0.044789
18	1.780007	1.601518	1.134646	0.030728
18	1.710696	1.833336	1.096591	0.023249
18	1.331607	2.483739	0.591253	0.029612
18	1.357593	1.968956	1.2092	0.017282
26	2.560157	2.19029	1.010075	0.084837
26	2.478865	2.142542	1.441704	0.160821
26	2.920662	2.166496	1.227926	0.177711
26	1.783109	1.700208	1.23534	0.205836
26	1.809358	2.395388	1.056138	0.105769
33	2.230052	2.81995	1.194645	0.540826
33	1.692464	2.038453	1.113628	0.428625
33	2.981684	2.168246	1.363852	0.486374
33	2.095491	1.58247	1.231077	0.474691
33	2.875616	2.102594	1.238574	0.612312
41	1.970818	2.333379	1.04227	1.296557
41	1.611026	1.927812	1.114056	1.438404
41	2.112647	2.279129	1.081485	0.99357
41	2.652937	1.953001	1.498288	1.30327
41	2.261238	2.34695	1.170614	1.306394
51	2.079631	1.228253	1.209477	2.075646
51	1.819921	1.666988	1.070121	1.644326
51	2.454389	2.202211	1.41537	2.439964
51	2.256488	2.134285	1.231388	1.709964
51	2.213276	2.102253	1.234634	1.884561
60	2.165804	2.18245	1.155609	2.283614
60	2.279157	1.885294	1.137585	1.698353
60	2.36829	2.52211	1.349542	2.049815
60	2.234632	2.281866	1.184983	1.165772
60	2.439225	1.996245	1.501995	2.82506
70	1.719859	2.411846	1.227642	1.786889
70	2.570555	2.462909	1.1756	1.878108
70	1.790253	1.887747	1.142104	1.895824
70	2.723166	2.042576	1.65201	1.8243
70	3.007495	2.227207	0.93787	2.226255
80	2.296889	2.001374	1.396972	2.20474
80	2.749139	1.714839	1.059392	1.594539
80	0.9041	2.298373	1.489557	2.267917
80	1.676455	1.788501	0.766479	2.491924
80	2.131265	1.738182	1.403356	1.898047

Table S1.4 – MAR estimates for the noisy LV dataset in Figs. 1 and S4

	MAR without transformation	MAR with log transformation	MAR with smoothing	MAR with log transformation and smoothing
β_{11}	-0.09089	-0.03360	1.06000	1.02000
β_{21}	0.27209	0.43560	0.13800	0.07940
β_{31}	-0.21012	-0.43570	0.07490	-0.10500
β_{41}	0.12619	0.42840	-0.33900	-0.22100
β_{12}	0.43295	0.24860	-0.05360	-0.01990
β_{22}	0.47619	0.62610	0.91000	0.94700
β_{32}	0.18150	0.17100	0.01730	0.12000
β_{42}	0.00788	0.23190	0.22900	0.19400
β_{13}	-0.20530	-0.01010	-0.01980	-0.01510
β_{23}	-0.28009	-0.33410	-0.07090	-0.07300
β_{33}	0.50995	0.57920	0.86700	0.90900
β_{43}	-0.00869	-0.02950	-0.03190	0.04240
β_{14}	0.07772	0.00960	-0.00954	-0.00439
β_{24}	0.06929	0.02720	-0.02780	-0.01270
β_{34}	0.00957	0.01530	-0.00911	-0.00807
β_{44}	0.93364	0.88740	0.98800	0.95600
α_1	1.70925	0.63980	0.01030	0.00614
α_2	0.67025	-0.04340	0.01430	0.01390
α_3	0.67931	0.29480	-0.00571	-0.00386
α_4	-0.17950	-0.45920	0.02010	0.04190
δ_1	0.22184	0.05270	0.00005	0.00001
δ_2	0.19571	0.07520	0.00014	0.00003
δ_3	0.01924	0.01480	0.00049	0.00028
δ_4	0.04708	0.07570	0.00005	0.00010

Table S1.5 – MAR estimates for the replicate LV dataset in Figs. 1 and S4

	MAR without transformation	MAR with log transformation	MAR with smoothing	MAR with log transformation and smoothing
β_{11}	0.77800	0.76500	1.01000	1.07000
β_{21}	0.07760	0.21000	0.00367	0.07720
β_{31}	-0.08920	-0.31200	-0.01630	-0.10700
β_{41}	0.09140	0.13400	0.23200	0.38400
β_{12}	0.13500	0.11600	-0.00781	-0.00292
β_{22}	0.87500	0.80500	0.93600	0.88300
β_{32}	0.14900	0.22500	0.10400	0.14800
β_{42}	-0.00518	0.17400	-0.08900	0.06510
β_{13}	0.24800	0.22200	-0.00982	-0.00328
β_{23}	-0.20400	-0.18300	-0.10300	-0.05940
β_{33}	0.94400	1.13000	0.86500	0.98300
β_{43}	0.01090	0.17500	-0.02880	0.04240
β_{14}	-0.02600	-0.01100	-0.02170	-0.00991
β_{24}	-0.00159	-0.00250	-0.00530	-0.00583
β_{34}	-0.00022	-0.00299	0.00004	-0.00317
β_{44}	0.97200	0.93000	0.96400	0.93000
α_1	0.02400	0.01470	0.00925	0.00610
α_2	0.02610	0.03690	0.01980	0.02190
α_3	-0.02240	-0.01470	-0.00880	-0.00573
α_4	0.02160	0.10700	0.02500	0.09300
δ_1	0.00557	0.00089	0.00008	0.00001
δ_2	0.00243	0.00073	0.00037	0.00009
δ_3	0.00001	0.00004	0.00024	0.00043
δ_4	0.00559	0.00267	0.00029	0.00022

Table S2.1 - MAR estimates for the noisy dataset in Fig. S3

	MAR without transformation	MAR with log transformation	MAR with smoothing	MAR with log transformation and smoothing
β_{11}	0.23009	0.01769	0.90100	0.93300
β_{21}	0.11849	0.16822	-0.18000	-0.10300
β_{31}	-0.18449	-0.35186	-0.26400	-0.61400
β_{41}	0.14318	2.18894	0.40800	1.05000
β_{12}	0.34796	0.23560	0.03870	0.01540
β_{22}	0.84182	0.75617	1.05000	0.94800
β_{32}	0.19214	0.17605	0.18600	0.20600
β_{42}	-0.03130	0.01950	-0.15300	-0.06350
β_{13}	0.21488	0.18478	-0.00110	0.00908
β_{23}	-0.04121	0.02412	-0.10500	-0.04810
β_{33}	0.78353	0.91531	0.87900	1.02000
β_{43}	0.01040	1.00320	-0.02870	0.05100
β_{14}	0.03493	0.01754	-0.00471	-0.00229
β_{24}	-0.00776	0.00115	-0.00050	-0.00170
β_{34}	-0.00548	0.00382	0.01160	0.01240
β_{44}	0.97027	0.81890	0.95100	0.91800
α_1	-0.00061	0.00073	0.01020	0.00586
α_2	0.02045	0.03086	0.02000	0.02130
α_3	-0.01764	-0.01187	-0.00431	-0.00279
α_4	0.02229	0.04416	0.02100	0.06150
δ_1	0.01953	0.00318	0.00001	0.00000
δ_2	0.01746	0.01414	0.00002	0.00000
δ_3	0.00158	0.00121	0.00002	0.00004
δ_4	0.00363	0.39522	0.00038	0.00007

Table S2.2 - MAR estimates for the replicate dataset in Fig. S3

	MAR without transformation	MAR with log transformation	MAR with smoothing	MAR with log transformation and smoothing
β_{11}	0.83000	0.81000	0.88600	0.87400
β_{21}	-0.06680	0.02220	-0.05350	0.04420
β_{31}	-0.12600	-0.35400	-0.09890	-0.39000
β_{41}	0.23600	0.37800	0.23500	0.41700
β_{12}	0.07710	0.04860	0.05470	0.04280
β_{22}	0.97800	0.89700	0.97600	0.90000
β_{32}	0.16200	0.19000	0.13100	0.19100
β_{42}	-0.07360	0.10500	-0.08250	0.08650
β_{13}	0.12900	0.11100	0.05310	0.06250
β_{23}	-0.06320	-0.03200	-0.09610	-0.06310
β_{33}	0.87400	1.02000	0.89000	1.06000
β_{43}	-0.04980	0.06360	-0.02580	0.08010
β_{14}	-0.00609	-0.00121	-0.00871	-0.00304
β_{24}	-0.00592	-0.00445	-0.00621	-0.00488
β_{34}	-0.00154	0.00406	-0.00073	0.00508
β_{44}	0.96100	0.92600	0.96300	0.92500
α_1	0.02250	0.01380	0.01240	0.00749
α_2	0.03120	0.04080	0.02220	0.02350
α_3	-0.02690	-0.01750	-0.00777	-0.00512
α_4	0.01850	0.10700	0.02520	0.09450
δ_1	0.00052	0.00004	0.00007	0.00001
δ_2	0.00029	0.00007	0.00004	0.00001
δ_3	0.00002	0.00000	0.00002	0.00001
δ_4	0.00219	0.00114	0.00039	0.00014

Table S3.1 – Initial conditions, parameter values and estimates for a four-variable LV system that converges to a stable steady state, as presented in Fig. S5

	Initial Condition	Estimate
X_1	1.2	1.20993
X_2	0.3	0.31991
X_3	2	1.82146
X_4	0.001	0.00104

	True Parameter Value	ALVI-MI
a_1	0.044	0.04398
b_{11}	-0.08	-0.07995
b_{12}	0.02	0.01997
b_{13}	0.08	0.07999
b_{14}	0	-0.00001
a_2	0.216	0.21599
b_{21}	-0.04	-0.04000
b_{22}	-0.08	-0.08001
b_{23}	0.04	0.04002
b_{24}	0	0.00000
a_3	0.116	0.11600
b_{31}	-0.16	-0.15993
b_{32}	0.16	0.15998
b_{33}	-0.08	-0.08007
b_{34}	0	-0.00001
a_4	0.2	0.20002
b_{41}	0	-0.00001
b_{42}	0	0.00000
b_{43}	0	0.00000
b_{44}	-0.1	-0.10000

	MAR	MAR with log transformation
β_{11}	0.89300	0.88800
β_{21}	-0.07190	0.08510
β_{31}	-0.17500	-0.43000
β_{41}	0.19200	0.42800
β_{12}	0.04840	0.03110
β_{22}	0.99000	0.91100
β_{32}	0.16800	0.18000
β_{42}	-0.05440	0.11000
β_{13}	0.06600	0.06700
β_{23}	-0.07540	-0.06800
β_{33}	0.91100	1.03000
β_{43}	-0.00639	0.03510
β_{14}	-0.00719	-0.00229
β_{24}	-0.00739	-0.00763
β_{34}	0.00126	0.00751
β_{44}	0.96300	0.92400
α_1	0.07320	0.05740
α_2	0.28900	0.01420
α_3	0.14200	0.20700
α_4	-0.22800	-0.38500
δ_1	0.00014	0.00006
δ_2	0.00004	0.00031
δ_3	0.00064	0.00020
δ_4	0.00032	0.00032

Table S3.2 – Initial conditions, parameter values and estimates for a four-variable LV system exhibiting damped oscillations as presented in Fig. S5

	Initial Condition	Estimate
X_1	0.3	0.3
X_2	0.3	0.3
X_3	0.4	0.4
X_4	0.6	0.6

	True Parameter Value	ALVI-MI
a_1	0.3	0.30245
b_{11}	-0.3	-0.30328
b_{12}	-0.27	-0.27098
b_{13}	-0.6	-0.60467
b_{14}	-0.045	-0.04708
a_2	0.4	0.40299
b_{21}	0.2	0.19592
b_{22}	-0.4	-0.40118
b_{23}	-0.4	-0.40578
b_{24}	-0.6	-0.60250
a_3	0.7	0.71519
b_{31}	-2.38	-2.39901
b_{32}	0.35	0.34344
b_{33}	-2.8	-2.82806
b_{34}	0.35	0.33650
a_4	0.6	0.60791
b_{41}	-0.96	-0.97003
b_{42}	-0.24	-0.24338
b_{43}	-0.96	-0.97466
b_{44}	-0.6	-0.60704

	MAR	MAR with log transformation
β_{11}	1.05000	0.98800
β_{21}	0.14700	0.01610
β_{31}	-0.25300	-0.07880
β_{41}	-0.23100	-0.05360
β_{12}	-0.08350	-0.11600
β_{22}	0.88800	0.92200
β_{32}	0.04880	-0.03410
β_{42}	-0.00228	-0.07260
β_{13}	0.03660	-0.04410
β_{23}	-0.07340	-0.06540
β_{33}	0.71200	0.89700
β_{43}	-0.20500	-0.02050
β_{14}	-0.10400	-0.01220
β_{24}	-0.12800	-0.03300
β_{34}	0.03690	-0.14100
β_{44}	0.96100	0.88100
α_1	0.04710	-0.22200
α_2	0.08150	-0.17700
α_3	0.06750	-0.56600
α_4	0.08660	-0.38800
δ_1	0.00000	0.00004
δ_2	0.00002	0.00016
δ_3	0.00015	0.00271
δ_4	0.00015	0.00065

Table S3.3 – Initial conditions, parameter values and estimates for a four-variable LV system displaying initially erratic oscillations, but converging to a limit cycle as presented in Fig. S5

	Initial Condition	Estimate
X_1	0.3	0.3
X_2	0.3	0.3
X_3	0.4	0.4
X_4	0.6	0.6

	True Parameter Value	ALVI-MI
a_1	1	0.98743
b_{11}	-1	-0.99101
b_{12}	-1.09	-1.08083
b_{13}	-1.52	-1.51341
b_{14}	0	0.01346
a_2	0.72	0.72230
b_{21}	0	-0.00274
b_{22}	-0.72	-0.72223
b_{23}	-0.3168	-0.31966
b_{24}	-0.9792	-0.97942
a_3	1.53	1.53466
b_{31}	-3.672	-3.67283
b_{32}	0	-0.00071
b_{33}	-1.53	-1.52615
b_{34}	-0.7191	-0.73207
a_4	1.27	1.27361
b_{41}	-1.5367	-1.53884
b_{42}	-0.6477	-0.64952
b_{43}	-0.4445	-0.44519
b_{44}	-1.27	-1.27581

	MAR	MAR with log transformation
β_{11}	0.87600	0.94673
β_{21}	0.26700	0.19269
β_{31}	-0.11100	-0.77772
β_{41}	-0.17600	-0.18648
β_{12}	-0.13600	-0.11408
β_{22}	0.90900	0.88847
β_{32}	0.03980	0.59990
β_{42}	0.06220	0.11789
β_{13}	-0.44100	0.00528
β_{23}	0.07280	0.01411
β_{33}	0.86500	0.93625
β_{43}	-0.03720	-0.00153
β_{14}	0.36500	0.00392
β_{24}	-0.19100	-0.17211
β_{34}	-0.02410	0.33444
β_{44}	0.93800	0.97758
α_1	0.02540	-0.12418
α_2	0.01980	-0.00507
α_3	0.03310	-0.28038
α_4	0.04680	-0.16530
δ_1	0.00001	0.00057
δ_2	0.00001	0.00012
δ_3	0.00013	0.00112
δ_4	0.00005	0.00022

Table S3.4 – Initial conditions, parameter values and estimates for a four-variable LV system displaying damped oscillations as presented in Fig. S5

	Initial Condition	Estimate
X_1	0.3	0.3
X_2	0.3	0.3
X_3	0.4	0.4
X_4	0.6	0.6

	True Parameter Value	ALVI-MI
a_1	0.3	0.27831
b_{11}	-0.3	-0.30250
b_{12}	-0.27	-0.25033
b_{13}	-0.6	-0.59705
b_{14}	-0.045	-0.00606
a_2	0.4	0.36675
b_{21}	0.2	0.19193
b_{22}	-0.4	-0.36840
b_{23}	-0.4	-0.40045
b_{24}	-0.6	-0.53672
a_3	0.7	0.64222
b_{31}	-2.38	-2.37532
b_{32}	0.35	0.39856
b_{33}	-2.45	-2.42900
b_{34}	0.35	0.44414
a_4	0.6	0.55927
b_{41}	-0.96	-0.96318
b_{42}	-0.24	-0.20356
b_{43}	-0.96	-0.95279
b_{44}	-0.3	-0.22817

	MAR	MAR with log transformation
β_{11}	0.96100	1.02036
β_{21}	0.17900	0.10195
β_{31}	-0.15100	-0.09094
β_{41}	-0.20000	-0.04845
β_{12}	-0.07430	-0.05021
β_{22}	0.94200	0.98452
β_{32}	-0.05210	-0.02708
β_{42}	-0.01790	-0.03530
β_{13}	-0.09270	0.00210
β_{23}	0.00417	-0.00943
β_{33}	0.82100	1.05860
β_{43}	-0.15000	0.02181
β_{14}	-0.00981	0.02438
β_{24}	-0.10400	-0.00099
β_{34}	-0.12500	-0.32180
β_{44}	0.96300	0.89997
α_1	0.05890	0.00507
α_2	0.01900	0.11510
α_3	0.13300	-0.41484
α_4	0.09470	-0.17804
δ_1	0.00003	0.00018
δ_2	0.00010	0.00101
δ_3	0.00014	0.00935
δ_4	0.00008	0.00056

Table S3.5 – Initial conditions, parameter values and estimates for a four-variable LV system displaying deterministic chaos (chaos 1) as presented in Fig. S5

	Initial Condition	Estimate
X_1	0.3	0.3
X_2	0.3	0.3
X_3	0.4	0.4
X_4	0.6	0.6

	True Parameter Value	ALVI-MI
a_1	1	1.01561
b_{11}	-1	-1.01294
b_{12}	-1.09	-1.10110
b_{13}	-1.52	-1.52409
b_{14}	0	-0.01741
a_2	0.72	0.72904
b_{21}	0	-0.00777
b_{22}	-0.72	-0.72674
b_{23}	-0.3168	-0.32100
b_{24}	-0.9792	-0.98775
a_3	1.53	1.48293
b_{31}	-3.5649	-3.52631
b_{32}	0	0.03573
b_{33}	-1.53	-1.50898
b_{34}	-0.7191	-0.67335
a_4	1.27	1.25074
b_{41}	-1.5367	-1.52127
b_{42}	-0.6477	-0.63310
b_{43}	-0.4445	-0.43667
b_{44}	-1.27	-1.25061

	MAR	MAR with log transformation
β_{11}	0.85600	1.00059
β_{21}	0.26400	0.20355
β_{31}	-0.16900	-0.79454
β_{41}	-0.21800	-0.23777
β_{12}	-0.14300	-0.10901
β_{22}	0.88800	0.88053
β_{32}	0.01640	0.59018
β_{42}	0.02020	0.08015
β_{13}	-0.47500	-0.03240
β_{23}	0.10500	0.03330
β_{33}	1.07000	0.76513
β_{43}	0.06420	-0.03995
β_{14}	0.38200	0.17765
β_{24}	-0.24000	-0.23158
β_{34}	-0.21500	0.90744
β_{44}	0.80900	1.08027
α_1	0.03510	0.01644
α_2	0.04320	-0.01131
α_3	0.11000	-0.11896
α_4	0.11500	-0.24402
δ_1	0.00002	0.00114
δ_2	0.00002	0.00015
δ_3	0.00022	0.00191
δ_4	0.00006	0.00024

Table S3.6 – Initial conditions, parameter values and estimates for a four-variable LV system displaying deterministic chaos (chaos 2) as presented in Fig. S5

	Initial Condition	Estimate
X_1	0.3	0.3
X_2	0.3	0.3
X_3	0.4	0.4
X_4	0.6	0.6

	True Parameter Value	ALVI-MI
a_1	0.3	0.29277
b_{11}	-0.3	-0.25379
b_{12}	-0.27	-0.28051
b_{13}	-0.6	-0.55795
b_{14}	-0.045	-0.07045
a_2	0.4	0.39048
b_{21}	0.2	0.26661
b_{22}	-0.4	-0.41601
b_{23}	-0.4	-0.33988
b_{24}	-0.6	-0.63818
a_3	0.8	0.77659
b_{31}	-2.38	-2.23922
b_{32}	0.35	0.31928
b_{33}	-2.45	-2.32117
b_{34}	0.35	0.27470
a_4	0.6	0.58578
b_{41}	-0.96	-0.86962
b_{42}	-0.24	-0.26048
b_{43}	-0.96000	-0.87774
b_{44}	-0.30000	-0.34969

	MAR	MAR with log transformation
β_{11}	1.05000	0.97700
β_{21}	0.00560	0.02030
β_{31}	-0.31600	-0.08880
β_{41}	-0.23000	-0.06400
β_{12}	-0.09830	-0.01780
β_{22}	0.99000	1.00000
β_{32}	0.08310	-0.02620
β_{42}	-0.01940	-0.01610
β_{13}	-0.00541	-0.06900
β_{23}	-0.12100	-0.07290
β_{33}	0.70200	0.87400
β_{43}	-0.18000	-0.05050
β_{14}	-0.08040	0.05960
β_{24}	0.00941	-0.02020
β_{34}	0.07400	-0.14500
β_{44}	0.97300	0.94100
α_1	0.05270	-0.11500
α_2	0.02820	-0.09870
α_3	0.07760	-0.53700
α_4	0.10200	-0.28000
δ_1	0.00000	0.00006
δ_2	0.00002	0.00023
δ_3	0.00009	0.00115
δ_4	0.00007	0.00025

Table S4.1 – ALVI-MI estimates for five experimental data examples from (Mühlbauer et al., 2020). Data came from experiments described in (Gause, 1934), (McLaren & Peterson, 1994) and (Huffaker et al., 1963). See R package gauseR (Mühlbauer et al., 2020) for datasets “gause_1934_science_f02_03”, “gause_1934_book_f32”, ”mclaren_1994_f03” and “huffaker_1963” for details on observations. Parameter estimates from Mühlbauer *et al.* can also be found in Table 2 in their paper.

Example 1 - *Paramecium caudatum* in monoculture. The slopes were estimated from an 8DF-spline from data without log transformation and ALVI-MI using a subsample of spline points at the 3rd and 12th days.

	Mühlbauer *et al.*	Estimate	Absolute Difference
a_1	1.259	0.92289	0.33611
b_{11}	-0.005	-0.00456	0.00044

Example 2 - *Paramecium caudatum* and *Paramecium aurelia* in a mixed population competition study. ALVI-MI was estimated from 10DF and 7DF-splines for *P. caudatum* and *P. Aurelia*, respectively. Spline points were taken at days 4, 8 and 11.

	Mühlbauer *et al.*	Estimate	Absolute Difference
a_1	1.259	0.98677	0.27223
b_{11}	-0.005	-0.00409	0.00091
b_{12}	1.259	-0.00649	1.26549
a_2	-0.005	0.79868	0.80368
b_{21}	1.259	-0.00136	1.26036
b_{22}	-0.005	-0.00536	0.00036

Example 3 - Predator-prey interactions between *Didinium nasutum* and *Paramecium caudatum*. ALVI-MI estimates were calculated using 14DF and 10DF-splines, respectively, using a subsample of the 122nd ,140th, 168th points of the second spline.

	Mühlbauer *et al.*	Estimate	Absolute Difference
a_1	1.099	1.70706	0.60806
b_{11}	-0.013	-0.03887	0.02587
b_{12}	-0.078	-0.11360	0.03560
a_2	-0.89	-1.27639	0.38639
b_{21}	0.084	0.14275	0.05875
b_{22}	-0.002	0.01565	0.01765

Example 4 - Multi-trophic dynamics for wolves, moose, and fir trees. ALVI-MI estimates were calculated using log-abundances and 8DF-splines. Spline points were chosen as a subsample corresponding to the years 1973, 1978, 1979 and 1982.

	Mühlbauer *et al.*	Estimate	Absolute Difference
a_1	0.01	-1.901823	1.91182
b_{11}	-0.003	0.028812	0.03181
b_{12}	0.00004	0.000003	0.00004
b_{13}	0	2.754448	2.75445
a_2	2.021	0.331244	1.68976
b_{21}	-0.088	-0.006836	0.08116
b_{22}	0	-0.000107	0.00011
b_{23}	0.002	-0.090569	0.09257
a_3	0.238	2.779411	2.54141
b_{31}	0	-0.051545	0.05154
b_{32}	-0.0002	0.000494	0.00069
b_{33}	-0.139	-4.693609	4.55461

Example 5 - Predator-prey interactions between *E. sexmaculatus* and *T. occidentalis.* ALVI-MI estimates were calculated using 15DF and 20DF-splines, respectively. The splines were constructed using log-abundances of the dependent variables, using a subsample of spline points corresponding to the 17^{th}, 48^{th} and 55^{th} datapoints.

	Mühlbauer *et al.*	Estimate	Absolute Difference
a_1	0.187	0.11148	0.07552
b_{11}	0	0.00003	0.00003
b_{12}	-0.028	-0.02960	0.00160
a_2	-0.377	-0.80007	0.42307
b_{21}	0.0012	0.00251	0.00131
b_{22}	-0.024	-0.03144	0.00744

Table S4.2 – ALVI-LR estimates for five experimental data sets from (Mühlbauer et al., 2020). Data came from (Gause, 1934), (McLaren & Peterson, 1994) and (Huffaker et al., 1963) experiments. See R package gauseR (Mühlbauer et al., 2020) datasets "gause_1934_science_f02_03", "gause_1934_book_f32", "mclaren_1994_f03" and "huffaker_1963" for details on observations. Parameter estimates from Mühlbauer *et al.* can also be found in Table 2 of their paper.

Example 1 - *Paramecium caudatum* in monoculture, analyzed with 8DF-spline

	Mühlbauer *et al.*	Estimate	Absolute Difference
a_1	1.259	0.93948	0.31952
b_{11}	-0.005	-0.00465	0.00035

Example 2 - *Paramecium caudatum* and *Paramecium aurelia* in mixed population, analyzed with 10DF and 7DF-splines

	Mühlbauer *et al.*	Estimate	Absolute Difference
a_1	1.259	0.85524	0.40376
b_{11}	-0.005	-0.00289	0.00211
b_{12}	-0.008	-0.00580	0.00220
a_2	1.026	0.84423	0.18177
b_{21}	-0.002	-0.00187	0.00013
b_{22}	-0.007	-0.00553	0.00147

Example 3 - Predator-prey interactions between *Didinium nasutum* and *Paramecium caudatum*, analyzed with 14DF and 10DF-splines

	Mühlbauer *et al.*	Estimate	Absolute Difference
a_1	1.099	0.45652	0.64248
b_{11}	-0.013	0.02117	0.03417
b_{12}	-0.078	-0.11495	0.03695
a_2	-0.89	-0.98922	0.09922
b_{21}	0.084	0.16549	0.08149
b_{22}	-0.002	-0.01146	0.00946

Example 4 - Multi-trophic dynamics for wolves, moose, and fir trees, analyzed with 28DF, 24DF and 28DF-splines

	Mühlbauer *et al.*	Estimate	Absolute Difference
a_1	0.01	-0.06509	0.07509
b_{11}	-0.003	0.00164	0.00464
b_{12}	0.00004	0.00007	0.00003
b_{13}	0	-0.13411	0.13411
a_2	2.021	0.20754	1.81346
b_{21}	-0.088	-0.00483	0.08317
b_{22}	0	-0.00009	0.00009
b_{23}	0.002	0.06010	0.05810
a_3	0.238	-0.08580	0.32380
b_{31}	0	0.00343	0.00343
b_{32}	-0.0002	-0.00020	0.00000
b_{33}	-0.139	0.43352	0.57252

Example 5 - Predator-prey interactions between *E. sexmaculatus* and *T. occidentalis*, analyzed with 15DF and 20DF-splines

	Mühlbauer *et al.*	Estimate	Absolute Difference
a_1	0.344	0.03525	0.30875
b_{11}	0	0.00038	0.00038
b_{12}	-0.059	-0.03619	0.02281
a_2	-0.236	-0.44687	0.21087
b_{21}	0.0005	0.00159	0.00109
b_{22}	0	-0.03540	0.03540

Table S4.3 – MAR estimates for five experimental data sets from (Mühlbauer et al., 2020). Data came from (Gause, 1934), (McLaren & Peterson, 1994) and (Huffaker et al., 1963) experiments. See R package gauseR (Mühlbauer et al., 2020) for datasets "gause_1934_science_f02_03", "gause_1934_book_f32", "mclaren_1994_f03" and "huffaker_1963" for details on observations. Parameter estimates from Mühlbauer *et al.* can also be found in Table 2 on their paper.

Example 1 - *Paramecium caudatum* in monoculture.

	MAR	MAR log transformation	MAR with data smoothing	MAR log transformation with smoothing
β_1	0.90000	0.85550	0.90400	0.74718
α_1	9.93000	0.15590	10.22600	0.21106
δ_1	287.57000	0.06920	126.15300	0.00525

Example 2 - *Paramecium caudatum* and *Paramecium aurelia* in coculture

	MAR	MAR log transformation	MAR with data smoothing	MAR log transformation with smoothing
β_{11}	0.81800	0.73590	0.91500	0.98309
β_{21}	0.07170	0.03240	0.11600	0.03625
β_{12}	-0.16030	-0.07020	-0.16900	-0.26372
β_{22}	0.82140	0.71450	0.87700	0.73153
α_1	27.54890	1.38260	0.91000	0.07810
α_2	20.30740	1.28150	5.82700	0.15430
δ_1	262.75870	0.17190	113.99000	0.03530
δ_2	253.59620	0.03470	11.12100	0.00202

Example 3 - Predator-prey interactions between *Didinium nasutum* and *Paramecium caudatum*

	MAR	MAR log transformation	MAR with data smoothing	MAR log transformation with smoothing
β_{11}	0.52400	0.80250	0.37800	0.86900
β_{21}	0.57700	0.10510	0.52100	0.18700
β_{12}	-0.57200	-0.21950	-0.45100	-0.25400
β_{22}	0.63300	0.59490	0.69100	0.76500
α_1	12.93300	-1.11100	0.40300	-0.75400
α_2	-2.76100	0.06450	0.23900	0.70000
δ_1	94.22700	10.97630	140.72600	7.15700
δ_2	27.95400	23.00840	83.62600	9.82300

Example 4 - Multi-trophic dynamics for wolves, moose, and fir trees

	MAR	MAR log transformation	MAR with data smoothing	MAR log transformation with smoothing
β_{11}	0.62900	0.69390	1.13000	1.17360
β_{21}	-4.15000	-0.04540	-3.48000	-0.04426
β_{31}	-0.00083	-0.02210	0.00137	0.07236
β_{12}	0.00517	0.07570	0.00148	0.01665
β_{22}	0.84800	0.86270	0.90300	0.89080
β_{32}	-0.00007	-0.12840	-0.00009	-0.13234
β_{13}	-27.30000	-0.34650	10.70000	0.22128
β_{23}	96.60000	0.08020	245.00000	0.13054
β_{33}	0.89000	0.89160	1.11000	1.06497
α_1	15.90000	0.12600	-0.35700	-0.02613
α_2	241.00000	1.18230	27.80000	0.02986
α_3	0.14200	0.85670	-0.00485	-0.01065
δ_1	32.30000	0.06210	3.88000	0.00553
δ_2	15000.00000	0.01080	1290.00000	0.00127
δ_3	0.00382	0.02160	0.00098	0.00591

Example 5 - Predator-prey interactions between *E. sexmaculatus* and *T. occidentalis*

	MAR	MAR log transformation	MAR with data smoothing	MAR log transformation with smoothing
β_{11}	1.01500	0.88120	1.11000	1.05163
β_{21}	0.00900	0.53850	0.00718	0.47337
β_{12}	-17.79700	-0.09960	-16.00000	-0.10626
β_{22}	0.56200	0.75520	0.73200	0.86330
α_1	94.24600	0.80680	0.47700	-0.00088
α_2	-1.28500	-2.86420	-0.02580	-0.01771
δ_1	15440.27300	0.13470	1360.00000	0.02078
δ_2	5.55100	0.33790	1.93000	0.08104

Table S5.1 – Synthetic MAR data

MAR Results

t	X_1	X_2	X_3	X_4
1	5	10	15	20
2	5.62418	35.2103	21.4125	10.3696
3	13.077	68.6603	16.2175	6.98986
4	30.8946	57.2944	7.75681	8.13234
5	42.7475	27.4855	3.71568	13.9927
6	31.3421	13.2593	2.63367	24.3619
7	16.5916	9.92497	3.02139	31.2622
8	9.868	12.4469	4.56419	27.4996
9	8.72248	20.3998	6.5998	19.5587
10	11.2768	30.657	7.33895	14.4998
11	16.7965	33.724	6.20514	13.314
12	21.9882	27.4413	4.66674	15.2345
13	22.1248	19.9474	3.79027	19.1227
14	18.0405	16.0646	3.69825	22.5386
15	14.0932	15.9557	4.22409	22.9275
16	12.3388	18.7495	5.03802	20.5772
17	12.7869	22.8183	5.59201	17.8653
18	14.8002	25.3774	5.51118	16.4484
19	17.1129	24.6804	4.99159	16.6605
20	18.1251	21.9731	4.48974	18.0462
21	17.3171	19.5701	4.27918	19.6396
22	15.6847	18.6862	4.39198	20.3941
23	14.456	19.3693	4.70288	19.9587
24	14.1822	20.9554	4.99681	18.8896
25	14.7787	22.3651	5.08888	17.9987
26	15.7517	22.7146	4.95911	17.7463
27	16.4482	21.9861	4.74141	18.1246
28	16.4701	20.8982	4.58774	18.7896
29	15.9468	20.1878	4.56995	19.2878
30	15.3325	20.1628	4.6678	19.3417
31	15.0101	20.6857	4.80099	19.0122

Table S5.2 –Synthetic MAR data with added noise (noisy MAR)

Noisy MAR data

t	X_1	X_2	X_3	X_4
1	0.7537	5.7537	10.7537	15.7537
2	3.6789	33.265	19.4672	8.42431
3	22.0484	77.6318	25.189	15.9613
4	27.8408	54.24056	4.70298	5.0785
5	44.2644	29.0024	5.23259	15.5096
6	27.0183	8.93558	0.005	20.0381
7	12.285	5.61827	0.005	26.9555
8	8.64674	11.2257	3.34294	26.2784
9	13.7228	25.4001	11.6001	24.559
10	9.55584	28.9361	5.61798	12.7788
11	19.8884	36.8159	9.29705	16.406
12	16.6399	22.093	0.005	9.88615
13	20.6563	18.479	2.32184	17.6543
14	15.1923	13.2165	0.85012	19.6905
15	12.7385	14.601	2.86941	21.5728
16	16.8878	23.2986	9.58707	25.1263
17	12.3928	22.4243	5.19791	17.4712
18	15.4333	26.0105	6.14431	17.0815
19	18.0468	25.6143	5.92554	17.5945
20	15.8709	19.7188	2.23545	15.7919
21	12.0743	14.3274	0.005	14.3969
22	14.4706	17.472	3.17787	19.18
23	14.9269	19.8403	5.17384	20.4297
24	17.9169	24.6901	8.73157	22.6243
25	13.8412	21.4276	4.15137	17.0612
26	14.6419	21.6048	3.8493	16.6365
27	22.3732	27.9111	10.6664	24.0496
28	13.6319	18.06	1.74954	15.9514
29	17.5022	21.7432	6.12531	20.8432
30	13.1904	18.0207	2.52572	17.1996
31	16.5325	22.2082	6.32346	20.5347

1121 **Table S5.3 – Synthetic MAR data with added noise replicates (replicate MAR)**

Replicate MAR data

t	X_1	X_2	X_3	X_4
1	4.49781	10.2631	14.7632	23.5471
1	5.11697	10.6373	13.2546	22.8581
1	4.17474	9.28028	15.2697	20.3851
1	4.79837	11.4797	15.3701	19.8827
1	4.61115	11.0217	12.2586	29.2412
3	11.9312	79.1524	17.0672	8.07106
3	10.947	62.6395	13.8815	7.31271
3	10.049	72.0532	15.922	9.44662
3	12.7162	67.1334	13.9795	6.6798
3	13.5553	74.391	19.6732	8.34617
5	41.8787	35.199	2.3953	15.7358
5	38.2823	34.7539	3.4456	17.6842
5	43.1218	17.1583	3.38346	9.12718
5	44.2767	37.916	2.02733	16.7366
5	30.7883	37.517	4.74218	11.6452
7	15.7223	9.78831	2.79243	47.4058
7	17.0225	8.50962	3.40691	32.5233
7	16.3596	9.74137	3.29265	24.6074
7	12.7344	13.1973	1.77531	31.342
7	12.9829	10.462	3.63077	18.2921
9	10.287	20.1958	4.824	12.0043
9	9.96034	19.7555	6.8854	22.756
9	11.7355	19.9764	5.86442	25.1459
9	7.16472	15.6769	5.89983	29.1256
9	7.27019	22.0869	5.04399	14.9662
11	15.6781	42.9179	5.62292	15.5585
11	11.8986	31.024	5.24159	12.3307
11	20.9623	32.9993	6.41934	13.992
11	14.7321	24.0842	5.79439	13.6559
11	20.2166	32.0002	5.82968	17.615
13	18.7011	21.639	3.34761	20.71
13	15.2871	17.8779	3.57818	22.9758
13	20.047	21.1359	3.47356	15.8704
13	25.1738	18.1115	4.81227	20.8173
13	21.4569	21.7648	3.75984	20.8672
15	12.942	9.13784	4.35658	25.9541
15	11.3257	12.4019	3.85461	20.5608
15	15.2742	16.3838	5.09822	30.5096
15	14.0426	15.8784	4.43551	21.3816
15	13.7737	15.6401	4.4472	23.5648
18	14.0831	25.677	5.31579	19.0626
18	14.8202	22.1809	5.23288	14.1771
18	15.3997	29.6731	6.20788	17.111
18	14.5306	26.8466	5.45091	9.73135
18	15.861	23.4862	6.90916	23.5824
22	11.7957	20.8907	4.50092	18.258
22	17.6303	21.3329	4.31011	19.19
22	12.2785	16.3511	4.18731	19.371
22	18.677	17.6922	6.05678	18.6402
22	20.6271	19.2914	3.43852	22.7473
26	15.8405	21.0941	5.80476	19.5684
26	18.9594	18.0741	4.40203	14.1525
26	6.23512	24.2245	6.18947	20.1291
26	11.5617	18.8505	3.18491	22.1173
26	14.6982	18.3201	5.83128	16.8463
30	10.6779	20.0665	4.69269	19.9748
30	16.5898	17.6329	5.2624	14.6922
30	19.4617	17.7483	5.08063	21.715
30	14.4153	13.7083	4.35089	17.093
30	14.1355	23.5724	5.30704	20.2612

Table S5.4 – Initial conditions and ALVI-MI parameters estimates for the synthetic MAR data

	Noise MAR	Replicate MAR
Spline	15DF-spline	15DF-spline
Point subsample	t = 2, 6, 15, 18, 26	t = 1, 3, 11, 13, 15
	Initial condition	Initial condition
X_1	0.814535	4.639806
X_2	7.333485	10.536398
X_3	12.89041	14.183246
X_4	14.301336	23.182858
Parameter	Estimate	Estimate
a_1	51.4374203	1.986927
b_{11}	-0.7981952	-0.029770
b_{12}	-0.1668495	-0.008283
b_{13}	-1.2191651	0.012518
b_{14}	-1.5223832	-0.068446
a_2	34.0728264	2.071364
b_{21}	-0.5711864	-0.054005
b_{22}	-0.1142499	-0.025029
b_{23}	-0.8100883	0.065384
b_{24}	-0.9677829	-0.051774
a_3	103.292766	0.327628
b_{31}	-1.7809655	-0.022297
b_{32}	-0.3029228	-0.008557
b_{33}	-2.6887155	-0.002260
b_{34}	-2.8840097	0.010410
a_4	30.8332588	-1.318063
b_{41}	-0.4422159	0.036978
b_{42}	-0.1141606	0.014019
b_{43}	-0.770332	-0.029955
b_{44}	-0.9159577	0.029689

Table S6.1 – Parameter values and initial conditions estimated for the 'grey whales' dataset (Gerber, Demaster, & Kareiva, 1999)

Results generated with ALVI-MI with 3DF-spline and a data sample composed of spline values in 1959 and 1966.

Parameter	True value	Estimate
ALVI-MI		
a_1		0.0948
b_{11}		-3.79E-06
$X_1(0)$	2894	3663.9550
MAR		
α_1		1260
β_{11}		0.943
δ_1		7240000
$X_1(0)$	2894	
MAR with log transformation		
α_1		1.0368
β_{11}		0.9512
δ_1		0.0327
$X_1(0)$	2894	
MAR with smoothing		
α_1		597
β_{11}		0.9930
δ_1		199000
$X_1(0)$	2894	
MAR with log transformation and smoothing		
α_1		0.4902
β_{11}		0.9535
δ_1		0.0014
$X_1(0)$	2894	

Table S6.2 – Parameters and initial conditions estimated for the 'Wolves and Moose' dataset (Vucetich, 2021)

Results of ALVI-MI with 15DF-splines and a data sample composed of spline values in 1991, 1994 and 1997.

ALVI-MI

	Initial condition	Estimate
X_1	20	21.6545
X_2	538	560.5340

Parameter		Estimate
a_1		-0.2732
b_{11}		0.0073
b_{12}		0.0001
a_2		0.8431
b_{21}		-0.0380
b_{22}		-0.0001

MAR with log transformation

	Initial condition	Estimate
X1	20	22.0000
X2	538	564.0000

Parameter		Estimate
β11		0.7670
β21		-0.1788
β12		0.0783
β22		0.8277
δ1		0.4485
δ2		0.1758

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