

## Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models

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**Abstract.** Long-term ecological data sets present opportunities for identifying drivers of community dynamics and quantifying their effects through time series analysis. Multivariate autoregressive (MAR) models are well known in many other disciplines, such as econometrics, but widespread adoption of MAR methods in ecology and natural resource management has been much slower despite some widely cited ecological examples. Here we review previous ecological applications of MAR models and highlight their ability to identify abiotic and biotic drivers of population dynamics, as well as community-level stability metrics, from long-term empirical observations. Thus far, MAR models have been used mainly with data from freshwater plankton communities; we examine the obstacles that may be hindering adoption in other systems and suggest practical modifications that will improve MAR models for broader application. Many of these modifications are already well known in other fields in which MAR models are common, although they are frequently described under different names. In an effort to make MAR models more accessible to ecologists, we include a worked example using recently developed R packages (MAR1 and MARSS), freely available and open-access software.

**Key words:** food webs; interaction strength; multispecies time series; reactivity; resilience; return rate; state-space models; VAR; vector autoregressive models.

### INTRODUCTION

Who eats whom? Which predators have the strongest cascading effects in an ecosystem? Which basal taxa provide the most important resources in a community? What might be the network of ecological repercussions when a particular nutrient decreases, a species is depleted or removed, or when temperature increases? How do these dynamics relate to ecosystem stability?

Diverse approaches to ecosystem modeling have been undertaken to address questions like these, in order to gain better understanding of trophic interactions and potential responses to human perturbations (Plagányi 2007). Such approaches include highly detailed and spatially explicit models, (e.g., ATLANTIS; Fulton et al. 2004), energy flow models based on diet estimates (e.g., EcoSim; Christensen and Walters 2004) or ecophysio-

logical parameters (e.g., Ecosys; Grant 2001), models of ecological communities as networks (Thébault and Fontaine 2010), and individual-based models (e.g., OSMOSE; Shin and Cury 2004). These approaches attempt to develop a mechanistic model of the system, and they require data (or assumptions) about diet, growth and biomass as well as the functional form of the interactions among species. The development of these mechanistic models can be challenging when such data are unavailable and possibilities for cross-validation are limited.

Alternatively, theoreticians, statisticians, and ecologists together have developed and applied statistical models of community dynamics using long-term abundance and environmental data. This approach is grounded in theory concerning the patterns of temporal correlation that emerge from species interactions (Ives 1995, Ives et al. 1999, 2003). Observational time series data are assumed to have been generated from a multivariate autoregressive (MAR) process. The core pieces of this model include a species interaction matrix

quantifying each species' interaction with itself (e.g., density dependence) and interactions with others (e.g., competition, predation), and another covariate matrix quantifying the impact of environmental drivers on species' per capita growth rates. These matrices are estimated from the time series data as an extension of simple linear regression, and the resulting matrices can be converted into estimates of interaction strengths and perturbation responses (Ives et al. 2003). Alternative MAR model structures, representing different functional groupings or presence/absence of specific interactions, can be compared using information theoretic approaches (such as Akaike's information criterion, AIC) that balance model "fit" with complexity (Burnham and Anderson 2010), and comparative metrics of community stability can be computed from the estimated model (Ives et al. 2003, Neubert et al. 2009). The MAR approach facilitates identification of key players and the pathways through which abiotic and biotic drivers affect population dynamics, and also addresses an important complication for other statistical analyses: reciprocal effects (e.g., Hampton and Schindler 2006). Reciprocal effects occur, for example, when predators eat prey "today" and directly reduce prey biomass, but then increase their own biomass "tomorrow" in response to the prey. In this case, the correlation between predator and prey abundances is both positive and negative, but statistical analyses that do not explicitly identify interaction pathways would fail to identify the reciprocal dynamics.

Ecological applications of MAR models are now well documented, and they have been used extensively to understand the dynamics of freshwater plankton communities. However, they have seen limited application outside the study of plankton communities and most ecologists are unlikely to be familiar with these models and their potential. Here we review the existing ecological applications, which are mainly, though not exclusively, in freshwater systems, and then discuss existing and potential extensions of MAR models that may make them more generally applicable for studying ecosystem and community dynamics.

#### The MAR model formulation

To characterize population growth, a discrete-time Gompertz model is used with log-linear density-dependence (Ives et al. 2003, Dennis et al. 2006). The stochastic univariate Gompertz equation written in log-space is

$$x_{i,t} = bx_{i,t-1} + a_i + w_{i,t} \quad (1)$$

where  $x_{i,t}$  is the natural log density of species  $i$  at time step  $t$ ,  $a$  is the intrinsic rate of increase for species  $i$ , and  $b$  represents the strength of density dependence ( $b = 1$  implies density independence,  $0 < b < 1$  implies undercompensation,  $b < 0$  implies overcompensation). The process error deviation,  $w_{i,t}$ , represents random deviations resulting from environmental or demographic

stochasticity from one time step to the next. Eq. 1 is a univariate, first-order, autoregressive, or AR(1), process. The AR(1) process can be expanded to include the effects of exogenous variables (i.e., covariates), such as abiotic drivers, on population dynamics. The following equation shows the form for a single time-varying covariate,  $u$ , with an interaction strength of  $c$ :

$$x_{i,t} = bx_{i,t-1} + a_i + cu_{t-1} + w_{i,t}. \quad (2)$$

If  $u$  were temperature, then  $c$  would represent how strongly (positively or negatively) temperature affects log-abundance.

To describe the stochastic dynamics of  $p$  interacting species and  $q$  environmental covariates, we use a multivariate version of Eq. 2, a MAR(1) model, which serves as a linear approximation for nonlinear stochastic multispecies processes (Ives et al. 2003). Hereafter, we drop the "(1)" for simplicity when referring to the model, and we use "species" to refer to the biotic groupings chosen by the user (e.g., "species" may be a guild of similar species). The MAR model is a system of  $p$  linear equations describing the abundances for each species in the community. In matrix form, the MAR model is written as follows:

$$\mathbf{x}_t = \mathbf{B}\mathbf{x}_{t-1} + \mathbf{a} + \mathbf{C}\mathbf{u}_{t-1} + \mathbf{w}_t \quad (3)$$

where  $\mathbf{x}_t$  is the  $p \times 1$  vector of log abundances for each of the  $p$  species at time  $t$ ,  $\mathbf{a}$  is the  $p \times 1$  vector of  $a$  values for each species,  $\mathbf{B}$  is a  $p \times p$  interaction matrix whose elements  $b_{ij}$  describe the effect of the density of species  $j$  on the per capita growth rate of species  $i$ ,  $\mathbf{u}_{t-1}$  is the  $q \times 1$  vector of covariate values at time  $t - 1$ , and  $\mathbf{C}$  is the  $p \times q$  matrix whose elements  $c_{ij}$  describe the effect of covariate  $j$  on species  $i$ . The vector of process errors  $\mathbf{w}_t$  is assumed to be drawn from a multivariate normal distribution with a mean of 0 and covariance matrix  $\mathbf{S}$ ; the selection of this distribution to describe the random stochasticity that populations experience has its roots in the statistical distribution that emerges from stochastic population dynamics (Ives et al. 2003, Holmes et al. 2007). It is important to note that inclusion of appropriate environmental drivers in  $\mathbf{u}$  may be necessary to remove non-stationarity from the residuals (e.g., seasonal patterns). For example, a covariate like temperature, measured properly, might be adequate to remove hourly patterns of activity in a reptile. In other cases, it might be necessary to include fixed seasonal effects using a covariate to specify month or season. Covariates need not be restricted to abiotic drivers. They may be biotic variables that are expected to affect  $x$  without exhibiting reciprocal effects in the analysis. For example, we would not expect fish abundance to respond to plankton abundance on a comparable time scale, so an estimated level of fish predation has been incorporated as a covariate in MAR models focused on plankton (Ives et al. 1999, Beisner et al. 2003).

*Parameter estimation, parameter uncertainty  
and model support*

One of the major goals of MAR modeling in ecology has been to estimate interspecific interaction strengths (**B**) in food webs and the effects of abiotic drivers on population dynamics (**C**) by fitting the MAR model to time series of species abundances. The majority of MAR applications have used one of two methods to estimate **B** and **C**: conditional least squares, which requires that data sets have no missing values, and maximum-likelihood. Bayesian approaches have been less frequently used in MAR modeling (cf. Mutshinda et al. 2009), though they can have some advantages. They more easily allow for non-Gaussian error structures or nonlinear process models, but depending on the circumstances, maximum likelihood may perform similarly to Bayesian approaches. Because MAR models are linear models with Gaussian error, the Bayesian solutions are nearly identical to those achieved with maximum likelihood, and Bayesian estimation may take longer to converge.

A second major goal of MAR modeling in ecology has been to reduce the food web model to a set of consistently strong interactions (represented by positive and negative values in **B** and **C**) and a set of least relevant interactions (represented by zeroes in the **B** and **C** matrices), accomplished by a model selection step. While it is possible to use a model with all **B** and **C** elements estimated, these models are typically prohibitively large and the uncertainty in the estimated elements would be high (Ives et al. 1999, 2003, Hampton et al. 2006). In some instances, a priori knowledge of the ecology of the system will help to identify zeroes (e.g., the direct effect of a carnivore on plants), and these zeroes can be set by the user. Otherwise, identification is accomplished with automated randomized search routines and information theoretic metrics, such as AIC (Burnham and Anderson 2010). These search routines construct thousands of MAR models with different **B** and **C** matrices by randomly setting the elements of these matrices to zero, and the models with the lowest AIC scores are identified. After this model search step, additional interactions may set to zero if they do not appear consistently in the candidate models, as defined by some threshold (e.g., 15% of the models [Ives et al. 1999]), or if bootstrapped confidence intervals overlap with zero (Hampton et al. 2006). Several top models may be considered separately, or models can be averaged to arrive at a final model.

The **B** and **C** matrices in the final MAR model can be viewed as a simplified model of the food web structure (species–species interactions) and its environmental drivers (species–environment relationships), respectively. These interaction strengths are driven by the correlation structure in the data and thus their interpretation is subject to the usual constraints on the interpretation of statistical correlations. Some identified relationships may actually be mutual correlations with

an unmeasured environmental driver that was not included in the model (Hampton et al. 2006), and some “real” interactions between taxa and their drivers may fail to emerge when they are relatively weak, complex, or inconsistent. Interpretation can be affected by choices about grouping taxa into size classes, trophic guilds or other functional groups, as is common in plankton studies. For example, the tiny freshwater zooplankton *Ascomorpha ovalis* has highly specialized feeding behaviors that allow it to exploit large dinoflagellates (Stelzer 1998), a group of algae mostly inedible to other zooplankton. The otherwise reasonable lumping of *A. ovalis* into “small grazers” and large dinoflagellates into “inedible algae” likely would obscure this relationship, unless these taxa are numerically dominant, in which case one might reach the generally wrong conclusion that small grazers thrive on large dinoflagellates. Similarly, incorrect relationships may emerge in MAR results when particular taxa act as proxies for unmeasured or obscured variables. In cases like these, the structure and interpretation of the model will rely crucially on the natural history expertise of the investigators.

*Ecosystem stability metrics from MAR models*

In the ecological applications to date, MAR models have been used primarily to assess interaction strengths and infer food web structure, but one can also use MAR modeling to compute stability properties of the system as a whole. Ives et al. (2003) describe a variety of different stability metrics, and we highlight three of these here.

- 1) The variance of the *stationary distribution* of community states relative to the variance of the process error. This property estimates the variability of the system at equilibrium relative to the process error variability that drives the stochasticity and is determined by the **B** (species interactions) and the **S** (process variances) matrices together. Stability increases as the ratio of the stationary distribution variance to process variance decreases.
- 2) The *return rate* of the system represents how quickly the community returns to its stochastic equilibrium after a disturbance. The return rate is determined by the dominant eigenvalue of the Kronecker product  $\mathbf{B} \otimes \mathbf{B}$ . Stability increases as return rate increases.
- 3) The *reactivity* of the system is an index of a community’s short-term response to perturbation. The “worst case” reactivity depends only on the eigenvalues of the estimated species interaction matrix **B**. Stability increases as reactivity decreases.

Even for relatively simple ecological systems, interpreting how individual elements of **B** translate into stability may be confusing; however, each of the above metrics offers the advantage of reducing stability to a single number (with confidence intervals). A further advantage is that these metrics are not obscured by the

magnitude of fluctuations. For example, in comparing the dynamics of a highly variable community and a community with low variability, one might immediately conclude that the highly variable community was less stable. Because the highly variable community might be simply reflecting a more variable environmental driver (e.g., temperature), the highly variable community in reality might be just as stable as the community with low variation. When relevant environmental drivers are included in the model, MAR analyses can cut through this overt variability to characterize the fundamental stability of the system; e.g., a MAR may reveal that a community exhibiting more variability is in fact more robust to perturbation than the community exhibiting lower variability.

#### *Previous ecological applications of MAR modeling*

In ecology, MAR modeling has been used to infer community dynamics primarily within aquatic sciences. Freshwater plankton communities have been a focus, in part due to frequent data collection and the nature of processing methods (Scheef et al. 2012). Perhaps more importantly, the information content of these time series typically is high; because plankton communities are short-lived, many generations can be represented in a relatively short study.

Previous MAR modeling of plankton data has demonstrated the range of ecological topics and problems that can be addressed using this approach. Analysis of long-term freshwater plankton data using MAR modeling has illuminated direct and indirect pathways through which plankton community dynamics are driven by keystone species. For example, Ives et al. (1999) constructed MAR models of plankton dynamics in a lake where planktivory rates had been manipulated by adding and removing fish, and found that *Daphnia pulex*, an important grazer, strongly influenced other species in the community through both direct and indirect interactions. Hampton and Schindler (2006) discovered an important influence of particular algal taxa (cryptomonads and picoplankton) on zooplankton growth that previously had not been considered when they applied MAR analysis to long-term data from Lake Washington. Several studies have characterized tight competitive or predatory linkages within freshwater plankton communities through MAR analysis. MAR analyses revealed strong predatory effects of an exotic fish on the structures of plankton communities in two Wisconsin lakes (Beisner et al. 2003) as well as strong grazing effects of zooplankton on primary producers in Lake Constance (Huber and Gaedke 2006) and lake mesocosms (Duffy 2007). Use of MAR modeling has facilitated the detection of competitive release between plankton groups during pH manipulations in mesocosms (Klug et al. 2000) and between *Daphnia* species during fungal parasite epidemics in small kettle lakes (Hall et al. 2009). MAR modeling has been used to characterize the pathways through which various

environmental factors, such as increasing temperature (Hampton et al. 2008), dissolved organic carbon and nutrient levels (Klug and Cottingham 2001), shifting pH (Fischer et al. 2001), and terrestrial carbon input (Carpenter et al. 2005) affect freshwater plankton communities. In these studies, MAR modeling both reinforced existing hypotheses about food web structure and suggested new, unexpected relationships among interacting biota.

In marine systems, there have been several applications of MAR modeling in fisheries sciences. These applications used the terminology vector autoregressive model (VAR), which is the name for a MAR model without covariates (Eq. 3 minus the **c** and **u**) in the econometrics literature. To the best of our knowledge, the first uses of MAR modeling to analyze marine fisheries data were applications involving the forecast of anchovy and sardine populations in the Mediterranean Sea (Stergiou 1991, Stergiou and Christou 1996). Since then, MAR modeling has been used to analyze the effects of climate and catch prices on fishing effort for albacore tuna, Chinook salmon, sablefish, and squid in California's Monterey Bay (Dalton 2001); to investigate the ecosystem linkages that affect the carite, croaker, and honey shrimp fisheries in Trinidad's Gulf of Paria (Dhoray and Teelucksingh 2007); to examine fish declines in the San Francisco Bay estuary (Mac Nally et al. 2010); to assess the portfolio effect in coral fishes (Thibaut et al. 2012); and to evaluate the effects of fishing pressure and environmental fluctuations on dynamics of commercially important cod (*Clupea harengus*) in the Black Sea with additional explorations of alternative management scenarios (Lindgren et al. 2009).

In terrestrial systems, MAR modeling has had limited application. MAR modeling has been used to study lynx-hare dynamics (Vik et al. 2008), to examine the effects of climate change on insect community dynamics (Yamamura et al. 2006), and to compare the relative importance of environmental stochasticity vs. stochasticity driven by interspecific-intraspecific interactions in rodents (Mutshinda et al. 2009). Given that trophic interactions and ecosystem stability are of similar interest across aquatic and terrestrial ecology, and that long-term data sets are available across systems, the scarcity of MAR use outside of freshwater ecology may be due to a lack of familiarity with MAR models and the ways in which they may be modified when data or questions do not conform with existing examples in the ecological literature.

As an illustration, consider the issues encountered when attempting to make the relatively small leap from applying MAR modeling with freshwater plankton systems to doing so with marine plankton systems (Francis et al. 2012, Scheef et al. 2012; Scheef et al., *in press*). In common marine data sets, compared to freshwater data, the investigator likely will find that observation error is higher due to both spatiotemporal



variation in sampling and the more “open” nature of marine systems. There also may be fewer data points available for each taxon, with possibly longer and uneven intervals between collections. These characteristics of multivariate time series are probably representative of a large number of ecological research programs; they do not exclude the possibility of applying MAR modeling, but do necessitate some modifications.

*Future directions to broaden MAR usability and applications*

Successfully applying MAR models to a broader diversity of long-term ecological data will require extending the MAR framework to explicitly accommodate (1) observation error, (2) spatially replicated time series across large geographic regions, (3) temporally nonuniform sampling, and (4) reduced autocorrelation structure, to accommodate varying “openness” of the system and monitoring schemes with long time lags between samples. State-space MAR models (MARSS) offer a framework for dealing with these issues.

MAR models that do not explicitly account for observation errors (Eq. 3) are limited to data sets where observation error can be safely ignored (Holmes et al. 2012b). When it cannot be ignored, separating process error from observation (measurement) error is critical because ignoring measurement error leads to the well-known consequence of spurious density dependence (Shenk et al. 1998, Knape and de Valpine 2012). In a MAR analysis, this phenomenon manifests as smaller estimates on the **B** diagonal when one uses a MAR analysis without observation error vs. one that includes observation error in the abundance estimates (see the Supplement for an example). Similarly, the off-diagonal terms of the **B** matrix (the inter-species interaction terms) tend to be smaller when observation error is important but not included. State-space MAR models combine a MAR model with an observation error model:

$$\mathbf{y}_t = \mathbf{Z}\mathbf{x}_t + \mathbf{D}\mathbf{d}_t + \mathbf{v}_t \quad (4)$$

where  $\mathbf{y}_t$  are the observations and are modeled as a linear function of the hidden species abundances,  $\mathbf{x}_t$ , and optionally environmental factors that affect observation error,  $\mathbf{d}_t$ . State-space MAR models are widely used in other fields (e.g., Durbin and Koopman 2012), and have been successfully employed in fisheries research (e.g., Lindegren et al. 2009, Hinrichsen and Holmes 2009). Although state-space MAR models allow one to include an observation model and estimate its variance, estimation of the **B** matrix in the face of unknown observation error is especially challenging (a fact alluded to in Ives et al. 2003) and comes at a cost in terms of higher variance in the **B** estimates. When measurement error variance is small relative to process error variance, a “standard” MAR model with no observation error component may actually improve the overall **B** estimation.

Where observation error is non-negligible, state-space models can be tailored to allow the user to maximally take advantage of the data at hand. For example, spatially distributed observations (spatial “replicates”) may be used to facilitate the separation of variances, an approach that has been successful in single-species process models (Humbert et al. 2009). Conceptually, this same approach could be applied to multiple species, treating communities as hierarchical or spatial replicates in a state-space MAR model. If the focus of inference is on species interactions, the process model (Eq. 3) could be constrained to share the **B** matrix across communities, with other parameters optionally shared depending on model assumptions.

State-space MAR models also allow greater flexibility in addressing temporal aspects of ecosystem dynamics—accommodating longer time lags in the process model as well as time-varying parameters. Eq. 3 shows a lag-1 MAR model, where  $\mathbf{X}_t$  depends on  $\mathbf{X}_{t-1}$ . A  $k$ th order MAR model, where  $\mathbf{X}_t$  depends on  $\mathbf{X}_{t-1}$ ,  $\mathbf{X}_{t-2}$ , ...,  $\mathbf{X}_{t-k}$ , can be re-written as a first-order model by re-defining the **B** matrix and **X** vector (see section 11.3.2 in Tsay 2010). State-space MAR models that include time-varying parameters are known more commonly as dynamic linear models (Shumway and Stoffer 2006). The ability to incorporate time-varying interactions in MAR models may be especially interesting to ecologists, recognizing that species interactions may change with species density, indirect effects, priority effects, a changing environment (Kordas and Dudgeon 2011), or through evolutionary change that occurs on ecologically relevant time scales (Hairston et al. 2005).

*Using MAR modeling*

Just as linear regression remains valuable to ecologists, even though more complex analytical tools are increasingly available, a standard MAR model will be useful in a variety of cases where the MARSS configuration is unnecessary or inappropriate. Two R packages have been developed that lower the technical barriers to fitting MAR and MARSS models to ecological data. The MAR1 R package (Scheef 2013) performs all aspects of fitting a MAR model to time series data and includes routines to do the critical model search steps. The Supplement shows complete worked examples, including an example of fitting a model with observation error. For fitting MAR state-space models, the MARSS R package is available and the user guide (Holmes et al. 2012a) includes many ecological case studies involving multivariate process models, including lag- $p$  models, with various observation models and a worked example of estimating interactions strengths with error-ridden species and covariate data.

MAR modeling provides a framework for inferring community structure, dynamics, stability and identifying environmental drivers using long-term time series data. With the maturation of many long-term ecological data sets across ecosystems worldwide, MAR modeling is a

method that should be broadly useful, particularly as new tools make it easier for ecologists to fit these models and modifications accommodate a greater diversity of ecological data sets and questions.

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#### SUPPLEMENTAL MATERIAL

##### Supplement

Applying MAR(1) and MARSS to an ecological data set ([Ecological Archives E094-247-S1](#)).