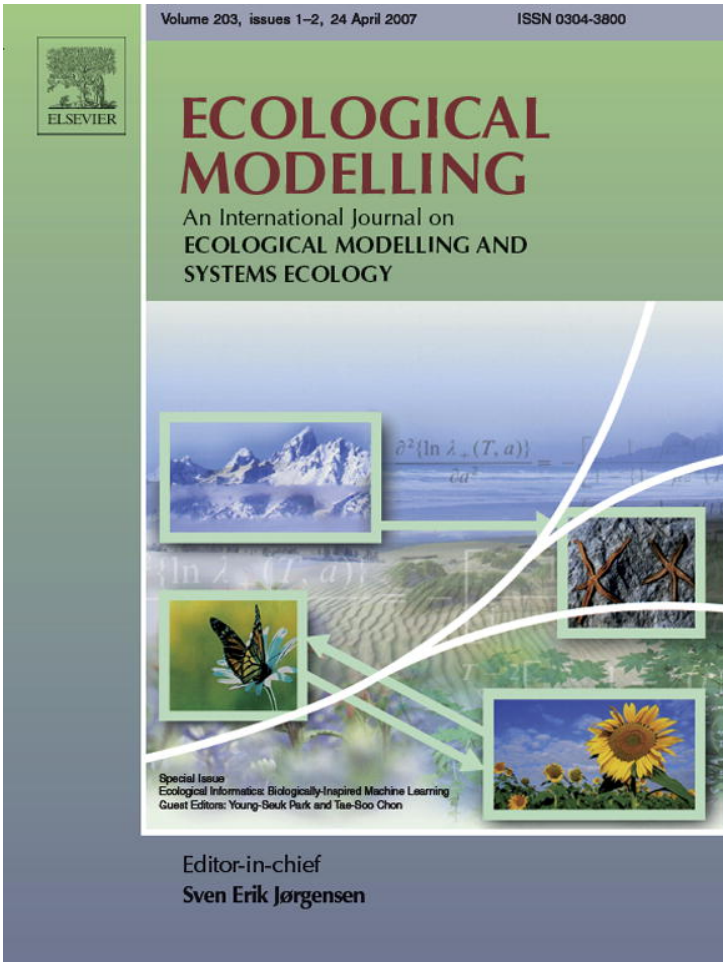

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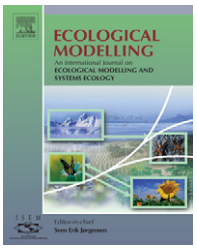

The role of sensitivity analysis in ecological modelling

J. Cariboni[a,b], *D. Gatelli*[a], *R. Liska*[a], *A. Saltelli*[a,*]

[a] *European Commission, Joint Research Centre, Via E. Fermi 1, 21027, Ispra, Italy*
[b] *K.U. Leuven, U.C.S., W. De Croylaan 54, B-3001 Leuven, Belgium*

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ABSTRACT

This work illustrates available best practices to run a sensitivity analysis for ecological models. The properties of recommended methods and their ranges of application are illustrated by applying the sensitivity analysis techniques to two test cases. The first one is a classic Lotka–Volterra model, while the second one is a study on a fish population dynamics. Both quantitative and qualitative approaches are applied and the differences between local and global techniques are highlighted by using the test cases.

1. Introduction

Mathematical models and computer simulations are developed by ecologists at different scales of resolution and levels of sophistication to study ecosystems and population dynamics. In some instances models help to corroborate or falsify hypothesis about the ecological system (e.g. is it true that a postulate model of ecological communities interprets the available evidence when uncertainties are weighted in? Are species in equilibrium with one another?). Often models are asked to answer specific questions about the present or future behaviour of the system under analysis (e.g. is extinction within a fixed time horizon a concrete threat?) or investigate interactions among model components (Zaldìvar et al., 1998).

The construction of a model is not a simple task; it is impossible to identify a single model structure for a natural system since the system is never closed and more than one model will be plausible given the evidence (Konikov and Bredehoeft, 1992; Oreskes et al., 1994; Beven et al., 1998). Further, models themselves are built under uncertainties in the values of the factors (e.g. the growth rate of a specific population), in the parameterization of the system (e.g. the boundary conditions of the dynamics) or in the choice of mutually exclusive scenarios (e.g. the choice of equations that describe dynamics). Finally, uncertainty can be related to an inherent stochasticity of the model (i.e. the dynamics includes a random term). Issues of parsimony in model identification are discussed in Young et al. (1996).

It is important to have a clear understanding of the types of uncertainty that the method addresses, to give a correct interpretation of the model results. Uncertainty associated with model structure and model parameters can be reduced by collecting more data, while uncertainty due to stochasticity in the population (variability) cannot be reduced by further study.

Methods considering multiple sources of uncertainty, such as model identification and parameter estimation, should allow the identification of the contribution of each source to the total predictive uncertainty (Wu and Tsang, 2004; Saltelli et al., 2000a,b, 2004).

In Fig. 1 some possible approaches to incorporate uncertainty propagation in the analysis are presented. The figure exemplifies a technique known as bootstrap (sampling with

* *Corresponding author*. Tel.: +39 0332 789686; fax: +39 0332 785733.
E-mail address: andrea.saltelli@jrc.it (A. Saltelli).
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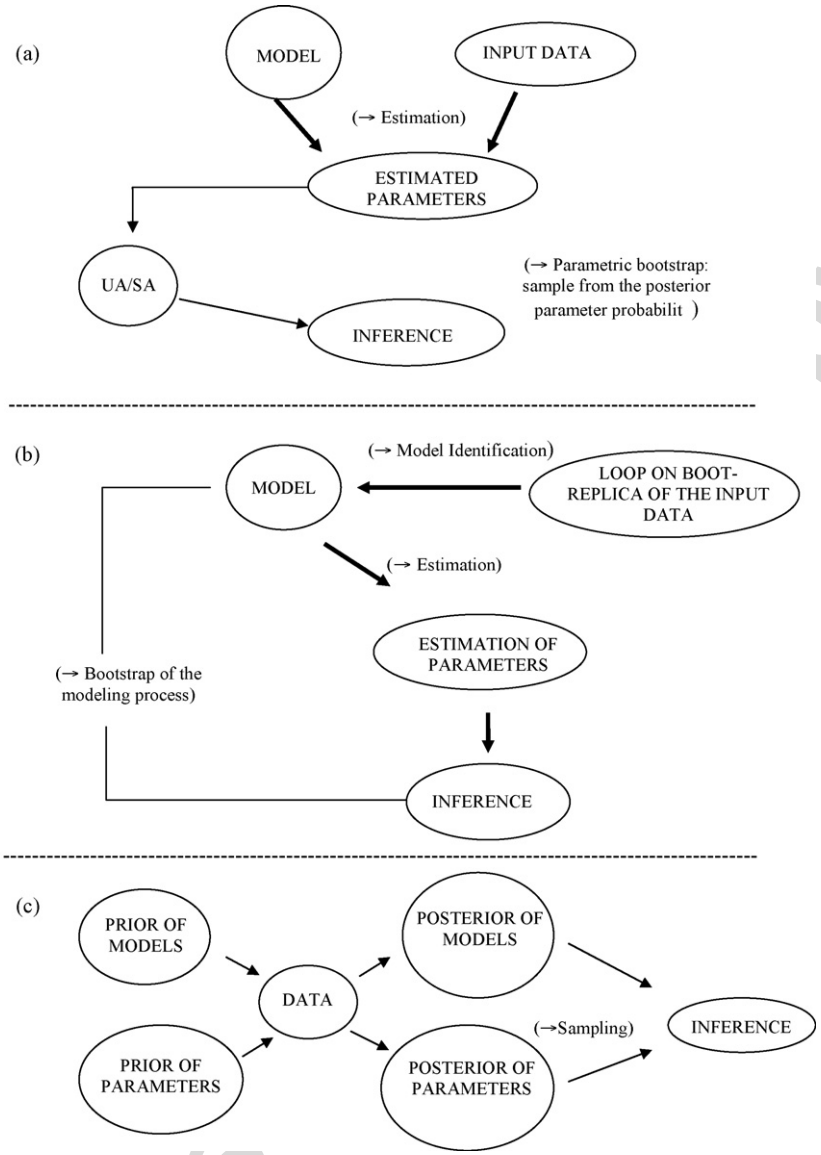

Fig. 1 – Schematization of the: (a) parametric bootstrap; (b) bootstrap of the modelling process; (c) Bayesian approach.

replacement). Either the bootstrap is applied to the model parameters (Fig. 1a) or directly to the data (Fig. 1b). In the first case, the model is assumed to be completely known, while in the second case it is identified through the bootstrap replicates (Chatfield, 1993). Fig. 1c illustrates the Bayesian approach, where the posterior distributions for the models and their parameters are estimated from their priors and from the data (see, e.g. Planas and Depoutot, 2000, and references therein, as well as Saltelli et al., 2004, p. 170).

Debates on the reliability of environmental models emerged both in the academy and among practitioners (Veld, 2000; Lomborg, 2001; Van der Sluijs, 2002). It has been argued that while the scientific methods dictate the methodology for drawing observations as well as the internal fabric of mathematical model, the process of inferring models from observations cannot be formalized scientifically (Rosen, 1991). Moreover, models that encode as much information as possible on a given structure can be judged as irrelevant because "they have many degrees of freedom and can be made to produce virtually any desired behaviour, often with both plausible structure and parameter values" (Hornberger and Spear, 1981). The main problem is that models cannot be validated (Konikov and Bredehoeft, 1992; Oreskes et al., 1994), but only confirmed or corroborated by demonstrating agreement between observations and predictions. Scientists are thus not supposed to reveal the truth by using models, but only to provide evidence (often expressed with probability) based on incomplete knowledge (Funtowicz and Ravetz, 1992). Further reading on the critique of models can also be found in Leamer (1990) and Funtowicz and Ravetz (1993, 1999).

In this view, uncertainty and sensitivity analysis (UA, SA) can help investigating the way uncertainties of different orders propagate on the output variables, and on the inference which the model is called to support. Uncertainty analysis quantifies the variability of the output caused by the incomplete knowledge or misspecification of the modeller.

Sensitivity analysis aims at establishing the relative importance of the input factors involved in the model, answering questions such as:

> "Which of the uncertain input factors are more influential in determining the variability affecting the inference?"
>
> "If the uncertainty of one of the inputs could be eliminated, which one should be chosen in order to reduce to the minimum the variance of the output of interest?"
>
> "Are there factors whose effect on the output is so low that they can be confidently fixed anywhere in their ranges of variation without affecting the results?"

Some methods are available to attempt answering such questions. These are the subjects of the present paper.

An overview of SA methodologies can be found in Saltelli et al. (2000a, 2004, 2005). Some relevant applications of SA techniques to ecological and environmental science include, e.g. atmospheric chemistry (Campolongo et al., 1999a,b), transport emissions (Kioutsioukis et al., 2004), geographic information systems (Crosetto and Tarantola, 2001), environmental management (EPA, 2003) and population dynamics (Zaldìvar and Campolongo, 2000; Fieberg and Jenkins, 2005).

The role of UA and SA is crucial in ecological risk assessment (see, e.g. Paustenbach, 2002), which applies analytical models to estimate the impact of human actions on natural resources and to interpret the significance of those effects in light of the uncertainties identified in each component of the evaluation process. The importance of characterizing the variability in the risk estimate to support public and private decisions is also a subject of debate. Stirling (1999) noted that risk assessments are often presented as crisp numbers conveying an idea of accuracy and precision that does not correspond to the assessment process.

Some effort has been put in understanding the correct role of SA from an environmental regulatory point of view. Both the report on *Good Practice Guidance and Uncertainty Management in National Greenhouse Gas Inventories* (EPA, 2003) and the *Draft Guidance on the Development, Evaluation, and Application of Regulatory Environmental Models* (IPCC, 2000) provide information about model use and model science in environmental settings. EPA (2003) also contains recommendations on good practices for UA and SA. In Europe, sensitivity analysis is mentioned in the guidelines for impact assessment (EC, 2005).

Another domain where UA and SA play a crucial role is that of composite indicators construction (Saisana and Tarantola, 2002; Saisana et al., 2005a). The request for a methodology that certifies the quality of composite indicators exploiting the use of UA/SA is exemplified by the *Environmental Sustainability Index* 2005 (Saisana et al., 2005b), which assesses a country's progress toward environmental sustainability in 141 countries worldwide.

The present work aims to present how SA techniques can be used in ecological modelling. Different SA techniques will be applied to two models for population dynamics, to illustrate the properties of the various techniques and the suggested domains of application. The paper's stance is a methodological one and the test cases used serve as illustrative (and simplified) examples.

The paper is organized as follows. Section 2 sketches an overview of SA techniques. Section 3 introduces two ecological models and presents the results of the application of some SA methodologies. Section 4 concludes.

2. Sensitivity analysis: an overview

2.1. *Characteristics of an ideal SA method*

In the following, a generic model is assumed to describe a natural system. The model is represented by a mapping f (a deterministic or stochastic function) which relates the inputs domain to the output space:

$$Y = f(X_1, X_2, \ldots, X_k).$$

The input factors (X_1, X_2, …, X_k) are supposed to be random variables described by identified probability distributions which reflect the uncertain knowledge of the system under analysis. Y is taken to be a scalar, i.e. even in the application we shall consider each output variable in turn.

If executed in accordance with available good practices, SA can help the modeller to measure model adequacy (e.g. does the model fit observation) and relevance (e.g. is the model-based inference robust), to identify critical regions in inputs space (e.g. which combination of factors corresponds to the highest risk), to detect interactions between factors, to establish priorities for research and to simplify the model structure.

As discussed in the reviews quoted in Section 1, an ideal SA methodology should be sensitive to the range of variation of each input factor and to the shape of its probability distribution. It should also operate simultaneously on all uncertain inputs, so that interactions among factors can be detected. A method is considered to be model independent (or model free) when it is not affected (or deceived) by non-linearities or non-additivities of the mapping f. Finally an ideal method should be able to treat groups of factors as single factors, allowing for a synthesis of the results and an easier interpretation.

A few heuristic settings for SA, each corresponding to a specific stage or need of the modelling process, are suggested in Saltelli and Tarantola (2002) and Saltelli et al. (2004). For instance, the aim of the SA experiment can be the identification of the most important factor/s which, if fixed to their true values, would lead to the greatest reduction in the variance of the output. This setting, known as factors prioritization setting, can be used for the prioritization of research, as it allows to identify (and rank) those factors which are most deserving of better measurement in order to reduce the output variance to the minimum. In general, since the true value of factors is not known before its measurement, the prediction of sensitivity analysis in priority setting will be of a probabilistic nature, e.g. "factor X_j seems to be the one that—on average, once fixed, would reduce the most the output variance". The purpose of this approach is to allow a rational choice under uncertainty (Saltelli et al., 2000a).

Another setting for SA can be that of screening non-influential factors in the model, i.e. identifying those factors that can be fixed at any given value in their domains without significantly reducing the output variance (factors fixing set-

ting). This setting is useful for model simplification or when the modeller has prior beliefs about the importance of some input factors, as it can help in proving or disproving a given model representation.

In other cases the objective of SA can be the reduction of the output variance to a lower threshold (*variance cutting setting*) by simultaneously fixing the smallest number of input factors. This setting could be of use when SA is part of a risk assessment study and e.g. when a regulatory authority was to find the width of the impact estimate distribution too wide. Note that the variance cutting and factor prioritization settings may appear to be very similar, as they both aim at reducing the output variance. However, in the case of factor prioritization the scope is to identify the most influent factors one by one, while in the variance cutting setting the objective is to reduce the output variance down to a pre-established level by fixing the smallest subset of factors at once.

Finally, the interest of the modeller can be to study which values of the input factors lead to model realizations in a given range of the output space, e.g. above or below an assigned threshold (*factors mapping setting*). For example, the analyst wishes to divide the realizations of the Monte Carlo simulation into two groups, e.g. by categorizing them as acceptable or non-acceptable. This setting can be carried out using the Smirnov test and the approach is known as Regionalized Sensitivity Analysis (RSA, Hornberger and Spear, 1981).

2.2. *Brief overview of the available methods*

The most common classifications of available SA methodologies distinguish between quantitative and qualitative methods and between local and global techniques.

Qualitative methods are aimed at screening, for example, a few active factors within a system with many non-influential ones. They do not give information on the relative difference of importance. *Quantitative* techniques can be designed to give information on the amount of variance explained by each factor. In general, the choice of which kind of method to use is driven by cost, as local or qualitative methods are computationally less expensive.

In *local* approaches (also known as one-at-a-time, OAT, methods) the effect of the variation of a single factor is estimated keeping all the others fixed at their nominal values (see, e.g. Rabitz, 1989; Turanyi and Rabitz, 2000; Cacuci, 2003 for applications).

Yet they cannot include the effect of the shape of the density functions of the inputs, and they are not model independent. Note that while in general all local methods are OAT, the reverse is not true, because on can vary one-at-a-time by a finite step of non-zero width.

Global approaches estimate the effect on the output of a factor when all the others are varying, enabling the identification of interactions in non-linear and/or non-additive models. Generally, global approaches allow the use of model-independent methods as they do not require assumptions of additivity or linearity. As a drawback, they are usually computationally expensive to estimate, while local methods can be set to produce system derivatives with a number of model simulations much lower than the number of derivatives to be estimated.

The simplest and most intuitive way to obtain a local sensitivity index is to compute derivatives (Tomovic and Vukobratovic, 1972; see Varma et al., 1999; Grievank, 2000 for recent review). The sensitivity of the output Y to a perturbation of an input factor X_i is estimated at a given value, X_i^*, as

$$Y'_{X_i} = \left.\frac{\partial Y}{\partial X_i}\right|_{X_i=X_i^*}.$$

In situations where Y and X_i have different ranges of uncertainty, a more balanced measure can be obtained normalizing the derivatives by the factors' standard deviations:

$$S^{\sigma}_{X_i} = \left.\frac{\sigma_{X_i}}{\sigma_Y}\frac{\partial Y}{\partial X_i}\right|_{X_i=X_i^*}.$$

The estimation of these local measures can be easily implemented (with the scope of assessing the relative importance of input factors) by solving systems of derivatives or taking incremental ratios, but they are informative only if the model is linear or if the range of uncertainty of the input factors is small, the latter condition often ensuring the former.

The Standardized Regression Coefficients (SRCs) can be viewed as an attempt to overcome shortcomings of local measures. Since they are built on regression analysis (see Section 3.1 for a detailed description) and based on Monte Carlo simulation, the SRCs reflect the shape of the probability distribution of each factor. Regression analysis allows also for the estimation of the model coefficient of determination, R^2, which represents the fraction of the output variance explained by the regression model itself. In the case of linear modelsg $R^2 = 1$ and the SRCs exactly quantify the amount of output variance explained by each factor; when models are moderately non-linear (i.e. $R^2 > 0.7$), the SRCs can be still used to qualitatively assess the factors' importance; finally, when R^2 becomes small, the SRCs cannot be considered as a reliable sensitivity measure. A typical example of failure of SRC is when the model is non-monotonic, e.g. when the scatterplot of Y versus an influent factor X_j is bell-shaped. In this case, SRC(X_j) can be small even if X_j is important. The quest for a method independent from linearity, additivity and monotonicity of the mapping has been satisfied by variance-based methods, developed starting from the principle of variance decomposition. The procedure for applying variance-based methods in numerical experiments is the same employed in the ANOVA in experimental designs (Box et al., 1978; Santner et al., 2003).

Different techniques have been used to decompose the output variance into the contributions imputable to each input factor. The most widely used are the Fourier Amplitude Sensitivity Test (FAST), and the Sobol' method. FAST (Cukier et al., 1973, 1978; Koda et al., 1979a; McRae et al., 1982; Sobol', 1990) decomposes the output variance V(Y) by means of spectral analysis:

$$V(Y) = V_1 + V_2 + \cdots + V_k + K$$

where V_i is the amount of variance explained by factor X_i and K is the residual (for some applications of FAST, see Koda et al., 1979b; Koda, 1982; Koda and Seinfeld, 1982; Liepmann and Stephanopoulos, 1985).

The Sobol' method is based on the same decomposition of variance, which is achieved by Monte Carlo methods in place of spectral analysis.

Both FAST and Sobol' methods estimate sensitivity measures which summarize the model behaviour. These measures concern the output sensitivity with respect to each factor individually and the total factor sensitivity inclusive of interactions. The most widely used measure, called the main effect or the first-order effect of factor X_i, is defined as:

$$S_i = \frac{V_i}{V(Y)}$$

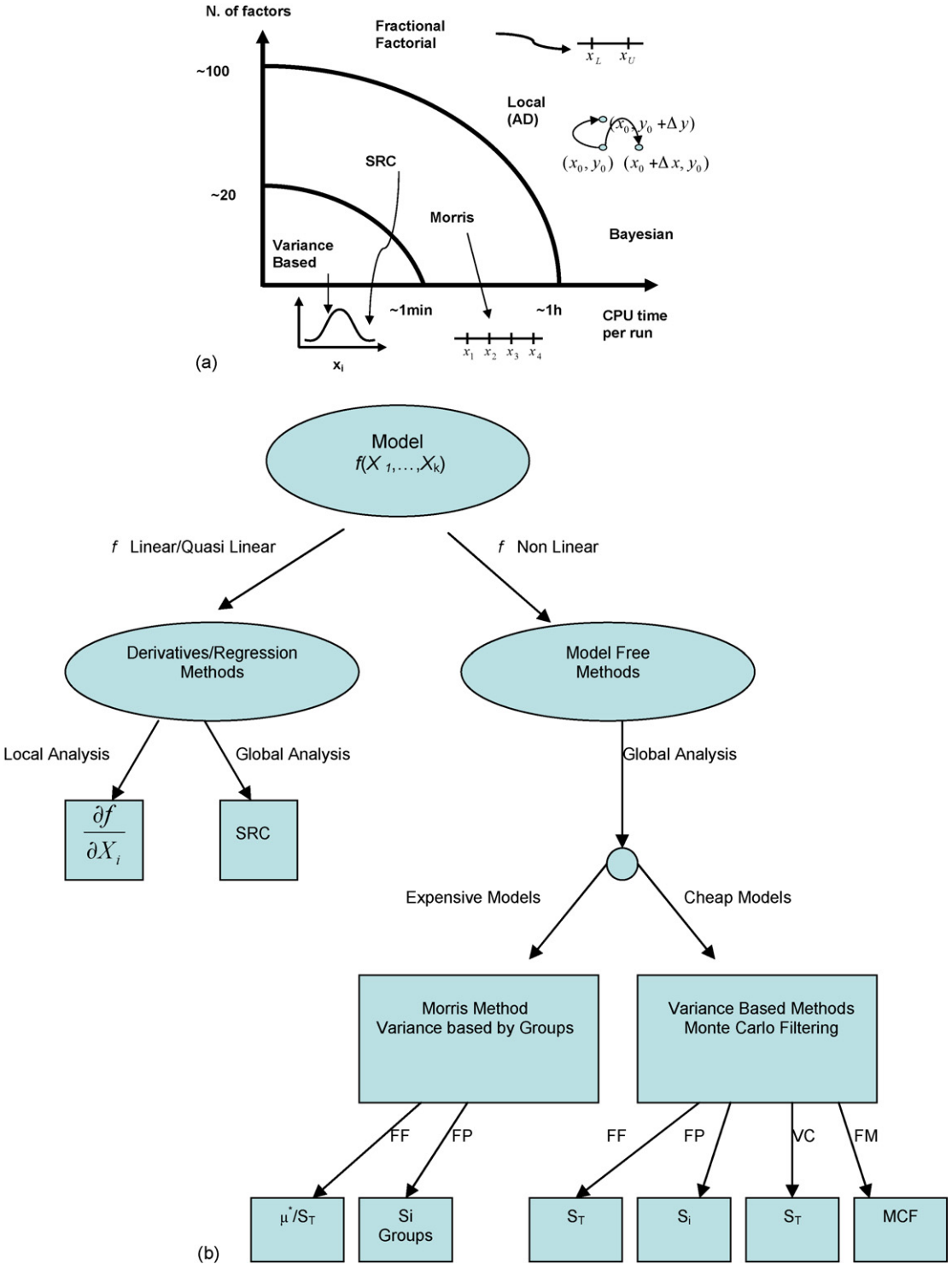

Fig. 2 – (a) Sketch of the various techniques available and their use as a function of computational cost of the model and dimensionality of the input space. AD means "automated differentiation". (b) Decision tree resuming the principal methods' characteristics and applications. MCF means "Monte Carlo Filtering", while FF, FP, VC and FM stand for "Factor Fixing", "Factor Prioritization", "Variance Cutting" and "Factor Mapping", respectively.

and can be shown to be the proper measure to use for factor prioritization setting (Saltelli and Tarantola, 2002).

Another useful measure describes the cases where the combined effect of two (or more) factors is greater than the sum of the individual effects, i.e. when the model is non-additive and interactions are present. In principle, interactions up to order k can be estimated but usually a synthetic measure is used. This measure is the total effect index ST_i (Homma and Saltelli, 1996) and it accounts for all the contributions to the output variation due to factor i (its first-order effect plus all its interactions). ST_i is effective for the factor fixing setting (see also Section 3.3).

Monte Carlo-based estimates of FAST sensitivity measures have been widely investigated, exploring the input space with techniques like Latin Hypercube Sampling or pseudo-random sampling (see, e.g. Hora and Iman, 1986; Iman and Hora, 1990; Ishigami and Homma, 1990; Krzykacz-Hausmann, 1990; Saltelli et al., 1993; Homma and Saltelli, 1996; McKay, 1996). The Sobol' and FAST approaches have been also improved to become computationally cheaper and easier to apply (Saltelli and Bolado, 1998; Saltelli et al., 1999, 2000b; Saltelli, 2002).

In cases where the model contains a large number of factors or/and it is computationally too expensive, the application of FAST or Sobol' methods is not possible. In these cases, the screening design developed by Morris (1991) and extended by Campolongo et al. (2006) can be used. This method is computationally cheaper, model free and can be used to identify non-influential factors (factor fixing setting). Nevertheless, it does not supply the variance decomposition obtained with the variance-based measures. The method is briefly described in Section 3.2.

Fig. 2 can be useful to choose among the different options, methods and procedures available for sensitivity analysis. Part (a) helps the user choosing the most suitable technique depending on the number of factors of the model and on the CPU time required to run it. Part (b) is a decision tree that leads to a suggested approach depending on the type of model (linear/non-linear, computationally cheap/expensive) and to an appropriate measure on the basis of the settings introduced above. Note that the computational cost of a model is determined by the number of runs (model evaluations) required, as the CPU time needed to compute the sensitivity measures once the model evaluations are available is usually negligible.

3. Applications

3.1. *Simple test case—Lotka–Volterra population model*

Lotka–Volterra population model (for a review, see May, 1976; Wangersky, 1978), is used here to present SA methods. The classical Lotka–Volterra predator–prey model with a stable solution describes the evolution of two species, one of which feeds upon the other, via the system of two partial differential equations:

$$\frac{dx_t}{dt} = rx_t\left[1 - \frac{x_t}{K}\right] - \alpha x_t y_t, \qquad \frac{dy_t}{dt} = -my_t + \theta x_t y_t. \tag{1}$$

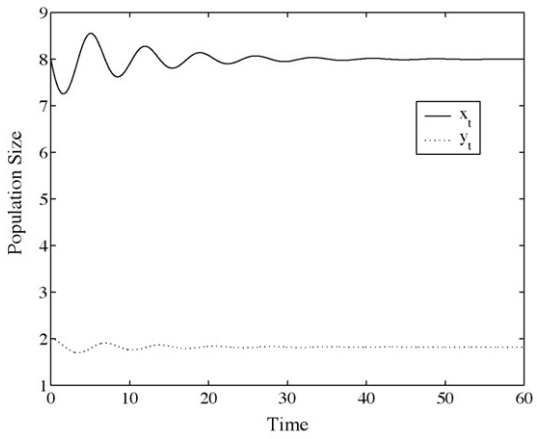

Fig. 3 – Evolution of the prey (x_t) and predator (y_t) populations estimated at the mean values of input factors.

Variables x_t and y_t denote the size of prey and predator populations, respectively, r the intrinsic rate of prey natural increase, α the proportionality constant linking prey mortality to the number of prey and predators, m the mortality rate of predators, θ the proportionality constant linking the increase in predators to the number of predators and prey, and K is a maximum number of preys that the environment can support.

The role of four uncertain input factors, r, α, m and θ, is analyzed. The following uniform distributions are assumed:

$$r \sim U[0.8, 1.8], \quad \alpha \sim U[0.2, 1], \quad m \sim U[0.6, 1],$$
$$\theta \sim U[0.05, 0.15]. \tag{2}$$

The constant K and the initial population sizes x_0, y_0 are treated as known constants

$$K = 50, \quad x_0 = 8, \quad y_0 = 2.$$

Note that by allowing the input factors to be independent random variables, the output factors, x_t and y_t, are also random variables.

The time evolution of x_t and y_t for the mean values of uncertain input factors, $r = 1.3$, $\alpha = 0.6$, $m = 0.8$, $\theta = 0.1$, is given in Fig. 3, where an equilibrium is observed.

The local sensitivities of x_t and y_t

$$\frac{\partial x_t}{\partial z}\,\frac{\partial y_t}{\partial z}, \qquad z = r, \alpha, m, \theta \tag{3}$$

and their squared normalized versions

$$\left(\frac{\sigma_z}{\sigma_{x,t}}\frac{\partial x_t}{\partial z}\right)^2\left(\frac{\sigma_z}{\sigma_{y,t}}\frac{\partial y_t}{\partial z}\right)^2, \qquad z = r, \alpha, m, \theta \tag{4}$$

with respect to the uncertain factors computed at their mean values are estimated. Fig. 4a and b plot the absolute values of the local sensitivities while the squared normalized measures are reported in Fig. 4c and d as a function of the time. σ_r, σ_α, σ_m and σ_θ are the standard deviations of r, α, m and θ, and $\sigma_{x,t}$ and $\sigma_{y,t}$ are standard deviations of x_t and y_t at time t, respectively.

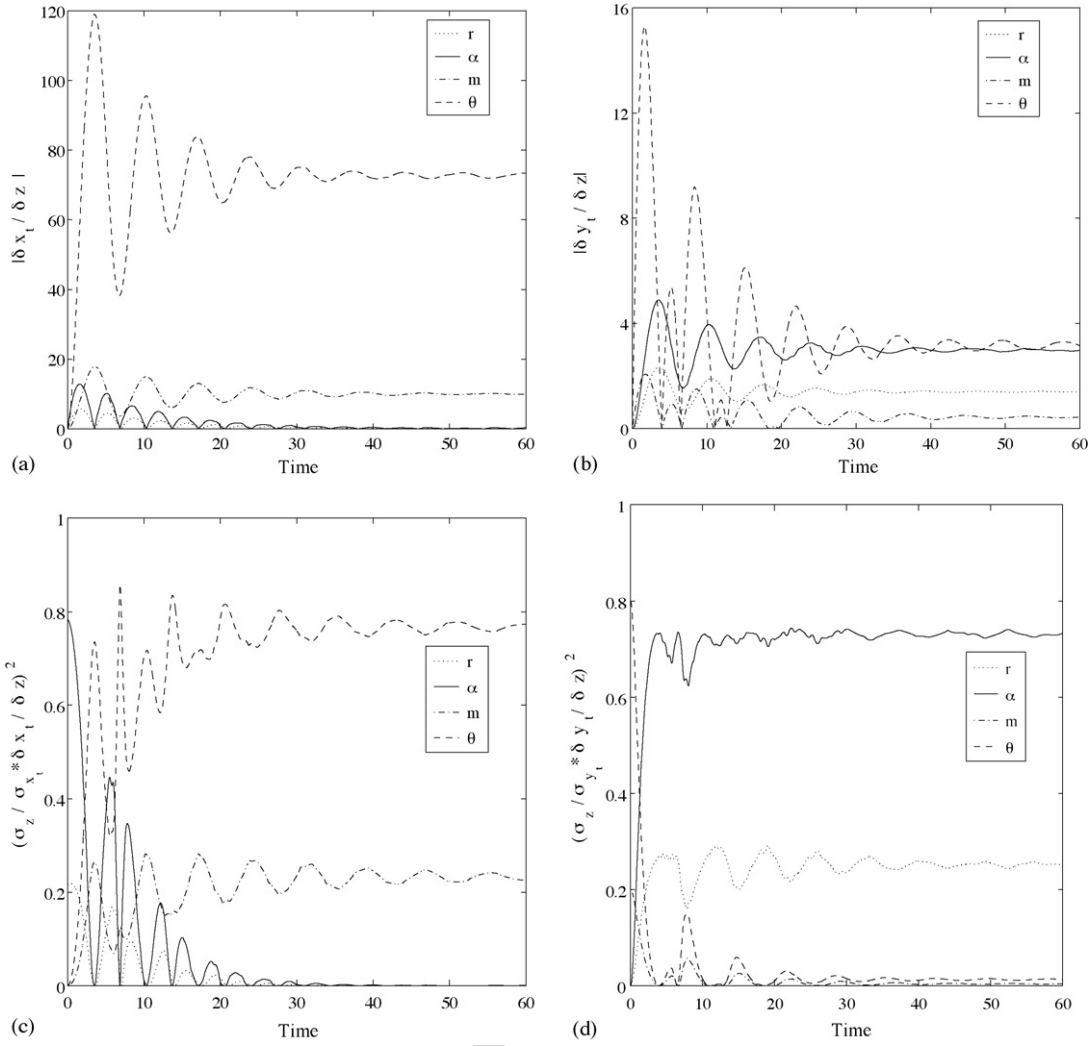

Fig. 4 – (a) Pure local sensitivity of x_t with respect to the factors r, α, m and θ, absolute value. z in the y axes label indicates the parameter r, α, m, θ, depending on the curve. (b) Pure local sensitivity of y_t with respect to the factors r, α, m and θ, absolute value. z in the y axes label indicates the parameter r, α, m, θ, depending on the curve. (c) Normalized local sensitivity of x_t with respect to the factors r, α, m and θ, absolute value. z in the y axes label indicates the parameter r, α, m, θ, depending on the curve. (d) Normalized local sensitivity of y_t with respect to the factors r, α, m and θ, absolute value. z in the y axes label indicates the parameter r, α, m, θ, depending on the curve.

The standard deviations $\sigma_{x,t}$ and $\sigma_{y,t}$ as shown in Fig. 4 are constructed using the approximation

$$\sigma^2_{x,t} \cong \sigma^2_r \left(\frac{\partial x_t}{\partial r}\right)^2 + \sigma^2_\alpha \left(\frac{\partial x_t}{\partial \alpha}\right)^2 + \sigma^2_m \left(\frac{\partial x_t}{\partial m}\right)^2 + \sigma^2_\theta \left(\frac{\partial x_t}{\partial \theta}\right)^2,$$

$$\sigma^2_{y,t} \cong \sigma^2_r \left(\frac{\partial y_t}{\partial r}\right)^2 + \sigma^2_\alpha \left(\frac{\partial y_t}{\partial \alpha}\right)^2 + \sigma^2_m \left(\frac{\partial y_t}{\partial m}\right)^2 + \sigma^2_\theta \left(\frac{\partial y_t}{\partial \theta}\right)^2. \quad (5)$$

Such an approximation is justified in linear systems and its adequacy is evaluated later.

The uncertainty of x_t and y_t is better captured by the normalized sensitivities than by the simple derivatives, since the former take into account the differences in the ranges of variation of the input factors. In particular, in our approximation (Eq. (5)), the squared normalized measures quantify the contribution of each factor to the output variance (Fig. 4c and d), which is in most cases the purpose of sensitivity analysis.

If we consider the prey population, θ is identified as the most important factor for $t > 10$ both by local and standardized local measures; in the transient phase ($t < 10$) θ is the most important factor at all times for the local measure while for the standardized local measures α is more important than θ at some points of time. For predators, α and θ are the most influential factors for the local measure while α and r are more significant in the standardized local approach. Note that while the relative importance of factors fluctuates in time in the pure local approach, the normalized local results are more easily interpretable for predators.

3.2. *Standardized regression coefficients*

The standard deviations of the output variables x_t and y_t for the computation of the normalized sensitivities are based on the linear approximation defined in Eq. (5). To check whether

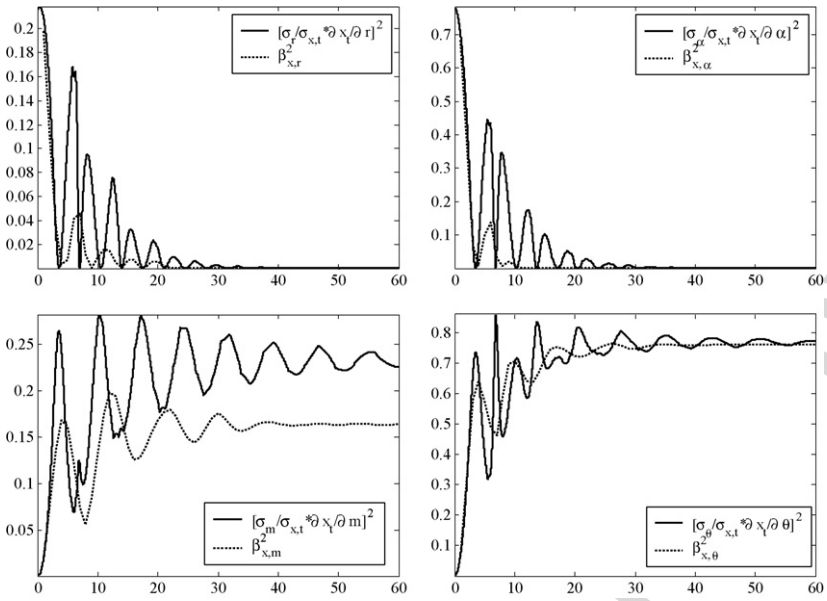

Fig. 5 – Squared normalized local sensitivity and squared SRCs of x_t with respect to the factors r, α, m and θ.

the model (1) is linear in its input factors the SRCs can be used (see Section 2.2). To this aim, a Monte Carlo simulation of the total computational cost of $C = 500$ independent runs from the distributions defined in (2) is performed. Indicating with r_d, α_d, m_d, β_d the input samples, with $x_{t,d}$ and $y_{t,d}$ the corresponding values of the output variables ($d = 1, \ldots, 500$), the following linear regressions are fit

$$x_{t,d} = b_{x,0} + b_{x,r}r_d + b_{x,\alpha}\alpha_d + b_{x,m}m_d + b_{x,\theta}\theta_d + e_{x,t,d},$$
$$y_{t,d} = b_{y,0} + b_{y,r}r_d + b_{y,\alpha}\alpha_d + b_{y,m}m_d + b_{y,\theta}\theta_d + e_{y,t,d} \quad (6)$$

at each point of time t.

Since these regression coefficients are dimensioned, it is common to use their standardized version, the SRCs:

$$\beta_{x,z} = \frac{\sigma_{x,t}}{\sigma_z} b_{x,z}, \qquad \beta_{y,z} = \frac{\sigma_{y,t}}{\sigma_z} b_{y,z}, \qquad z = r, \alpha, m, \theta.$$

For linear models, $(\beta_z)^2$ provides the fraction of the output variance due to factor z. Using the SRCs to assess the contribution of each factor to the output variability leads to different results with respect to the local measures in the transient phase of the system. For instance, for the prey population at $t = 8$ both local measures identify m as the most important factor, while the most significant factor is θ when using the squared SRCs. Note that the squared normalized local measures are equal to the squared SRCs for linear models, but even for partially non-linear models they differ from one another. In fact, while the normalized local measures are evaluated at single fixed points, the SRCs are estimated exploring the input space of each input factor, capturing the non-linear model features. Figs. 5 and 6 plot the $(\beta_z)^2$ together with squared normalized local measures for the Lotka–Volterra model.

Note that if the factors are independent and the true model (1) is linear, then the following equalities hold (see Draper and Smith, 1981):

$$(\beta_{x,r})^2 + (\beta_{x,\alpha})^2 + (\beta_{x,m})^2 + (\beta_{x,\theta})^2 = 1,$$
$$(\beta_{y,r})^2 + (\beta_{y,\alpha})^2 + (\beta_{y,m})^2 + (\beta_{y,\theta})^2 = 1. \quad (7)$$

The sum of $(\beta_z)^2$ therefore serves as a check of the model linearity. This sum is known also as the model coefficient of determination which can be computed as:

$$R^2_{x,t} = \sum_{d=1}^{500} \frac{(x^*_{t,d} - \mu_{x,t})^2}{(x_{t,d} - \mu_{x,t})^2}, \qquad R^2_{y,t} = \sum_{d=1}^{500} \frac{(y^*_{t,d} - \mu_{y,t})^2}{(y_{t,d} - \mu_{y,t})^2}.$$

$\mu_{x,t}$ and $\mu_{y,t}$ are the mean values of x_t and y_t, and $x^*_{t,d}$ and $y^*_{t,d}$ are fitted values based on Eq. (6). As can be seen from Fig. 7, the coefficients of determination of x_t and y_t are above 0.7, with the exception of x_t at $t = 8$. At the equilibrium R^2 is above 0.9 for x_t and above 0.8 for y_t. The linearity of the model is therefore higher at the equilibrium than at the transient stage. It follows that the use of the local measure is not fully justified in the transient phase.

The price one pays using a computationally cheaper sensitivity measure, e.g. a normalized local measure, instead of the more expensive global sensitivity measures is a loss of information in the non-linear part of the model. In general it is useful to perform a regression analysis as a preliminary step in SA. It may happen that the relationship between input and output variables is not monotonic and/or that interactions are part of it. This can lead to a low value of R^2 as discussed. When this happens one needs either to search for non-linear regression models (see, e.g. McCarthy et al., 1995, 1996 for the application of a logistic regression to a population viability model), or to apply a model-free global sensitivity approach (see next section).

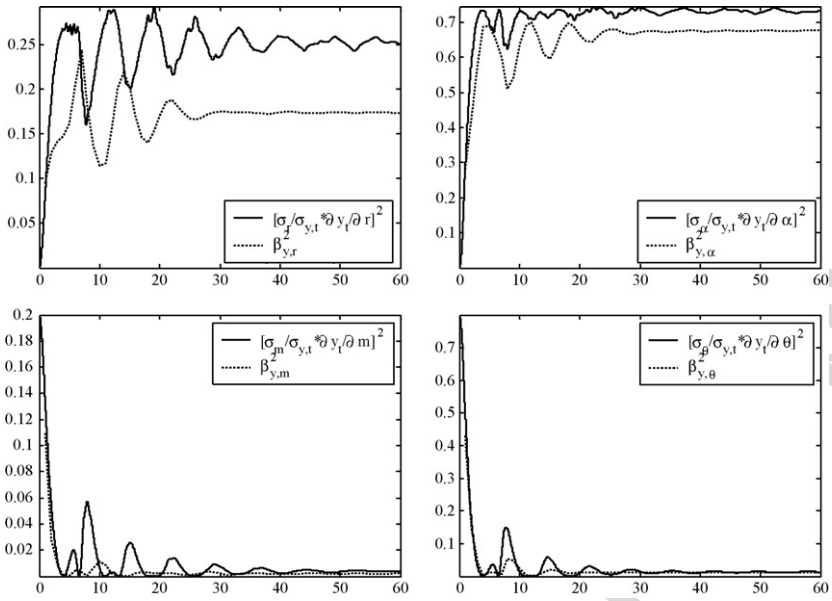

Fig. 6 – Squared normalized local sensitivity and squared SRCs of y_t with respect to the factors r, α, m and θ.

3.3. *Variance decomposition-based sensitivity measure—method of Sobol'*

The basic idea of Sobol' method (Sobol', 1990) is to decompose the function $f(X_1, \ldots, X_k)$ into terms of increasing dimensionality, namely

$$f(X_1, \ldots, X_k) = f_0 + \sum_{j=1}^{k} f_j(X_j) + \sum_{1\le j<l\le k} f_{jl}(X_j, X_l) + \cdots + f_{1,2,\ldots,k}(X_1, \ldots, X_k). \quad (8)$$

If the input factors are mutually independent then there exists a unique decomposition of (8) such that all the summands are mutually orthogonal. The variance of the output variable Y can be therefore decomposed into:

$$V(Y) = \sum_{j=1}^{k} V_j + \sum_{1\le j<l\le k} V_{jl} + \cdots + V_{1,2,\ldots,k} \quad (9)$$

where $V_j, V_{jl}, \ldots, V_{1,2,\ldots k}$ denote the variance of $f_j, f_{jl}, \ldots, f_{1,2,\ldots,k}$, respectively. In this approach the first-order sensitivity index for factor X_j defined in Section 2.2, is given by:

$$S_j = \frac{V(E(Y|X_j))}{V(Y)} = \frac{V_{x_j}(E_{x_{\sim j}}(Y|X_j))}{V(Y)} \quad (10)$$

where E and V indicate, respectively, the mean and variance operators and $\sim j$ indicates all factors but j. The inner expectation is taken at a generic point in the space of variable X_j, while the outer variance is over all possible values of this generic point.

The higher order sensitivity indices $S_{j_1,\ldots,j_s}$ are given by

$$S_{j_1,\ldots,j_s} = \frac{V_{j_1,\ldots,j_s}}{V(Y)}$$

for $s > 1$. Eq. (9) can be rewritten in terms of sensitivity indices as:

$$1 = \sum_{j=1}^{k} S_j + \sum_{1\le j<l\le k} S_{jl} + \cdots + S_{1,2,\ldots,k}.$$

The total order effect ST_j is instead given by:

$$ST_j = \frac{E(V(Y|X_{\sim j}))}{V(Y)}. \quad (11)$$

Note that this time the inner variance is over all possible generic values of X_j while the outer mean is over the space $X_{\sim j}$. In Saltelli (2002) a computationally efficient design is dis-

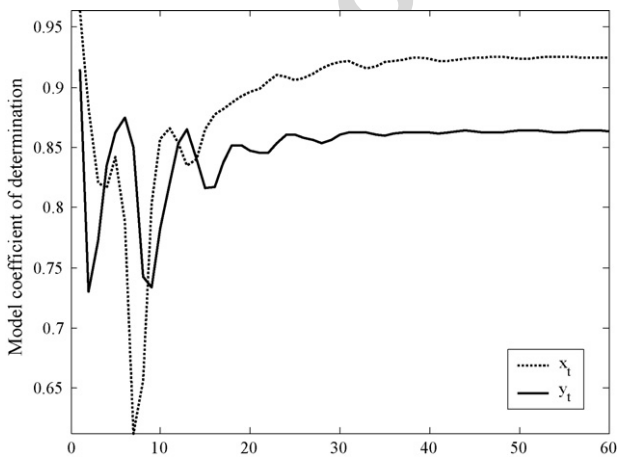

Fig. 7 – Evolution of the coefficient of determination for predator and prey populations.

Table 1 – Sobol' first and total order sensitivity indices for the predator and prey populations at two different times

	x_t prey		y_t predator	
	$t=8$ (%)	$t=60$ (%)	$t=8$ (%)	$t=60$ (%)
Sobol' S_i				
S_r	5.4	0.0	18.9	16.1
S_α	1.8	0.0	57.7	77.4
S_m	4.6	16.2	0.6	0.2
S_θ	62.1	82.4	4.5	1.5
$S_r+S_\alpha+S_m+S_\theta$	74.0	98.7	81.8	95.3
Sobol' ST_i				
ST_r	26.9	0.0	35.5	20.3
ST_α	21.9	0.0	73.5	81.8
ST_m	12.0	18.0	2.7	0.5
ST_θ	71.7	84.2	12.0	2.2

$t=8$ is representative for the transitional stage; $t=60$ is representative for the equilibrium stage.

cussed, which allows to estimate the $\{S_j, ST_j, j=1, 2, \ldots, k\}$ at the computational cost of

$$C = m(k+2) \tag{12}$$

where m is the Monte Carlo sample size used to estimate the integrals in definitions (10) and (11).

For our Lotka–Volterra model (1) the first-order sensitivity indices and total sensitivity indices based on $C=12.288$ ($m=2.048$) draws are computed at time $t=8$ and 60, see Table 1. For the prey population the first-order indices explain 74% of the total variance at time $t=8$ and the most influential is parameter θ. For the predator population, the first-order indices account for more than 81% of the total variance. At the equilibrium ($t=60$) almost 99% of the variance of the prey population size and 95.3% of the variance of predator population size are explained by the first-order effects. These results confirm that a model-free sensitivity analysis is useful for the transient phase, where the contributions of interactions to the variance are, respectively, 26% and 19% for prey and predator populations. On the other hand, the model is almost linear at equilibrium and a local analysis can be suitable.

Note that the classical Lotka–Volterra model used in the present example can be easily extended for the inclusion of a stochastic term (Goel et al., 1971; Vilar and Solé, 1998):

$$\frac{dx_t}{dt} = rx_t\left[1-\frac{x_t}{K}\right] - \alpha x_t y_t + f_x(x,y)\xi_x(t),$$
$$\frac{dy_t}{dt} = -my_t + \theta x_t y_t + f_y(x,y)\xi_y(t). \tag{13}$$

where $\xi_i(t)$ ($i=x, y$) are (correlated) random processes (e.g. Brownian motions) and the terms $f_i(x,y)\xi_i(t)$ ($i=x, y$) model the contribution of a noise term which may, for instance, represent a fluctuating growth rate.

In this case, the sensitivity analysis can be conducted to account for the contribution of the stochastic term as a separate factor. To this aim, a number of realizations of the random processes is generated and a trigger factor is used to select one couple of elements (one from the predators, the other from the preys) for each run of the Monte Carlo simulation. The sensitivity analysis indices can be estimated as described above, the contribution of the noise term being described by the sensitivity indices of the trigger factor.

In general, whenever there is sufficient information, it is better to build a stochastic model; if not, deterministic models can be carefully used to gain insight into stochastic sensitivities (Caswell, 1989).

This is an important aspect to be considered, as many population dynamic models in ecology are in fact stochastic (the environment, together with vital rates, vary randomly over time).

3.4. *A model for fish population dynamics*

A model for the dynamics of pelagic fish ecosystems is given in Zaldìvar et al. (1998). The model describes the time evolution of an ecosystem with three species of fishes: sardines, anchovies and mackerels. The dynamics are governed by the Lotka–Volterra difference equations and a stage-based approach is chosen, i.e. the life cycle is defined in terms of size classes rather than age classes (Caswell, 1989). Detailed information on the model is given in Zaldìvar and Campolongo (2000).

Table 2 – Stage life history factor values of the Pacific sardine (Smith et al., 1992)

Stage	Daily mortality		Duration (days)		Daily fecundity	
	Min	Max	Min	Max	Min	Max
Egg	0.310	2.12	1.4	3.9	0	0
Yolk-sac larvae	0.394	0.971	1.4	3.9	0	0
Early larvae	0.1423	0.3502	5	21	0	0
Late larvae	0.057	0.139	20	50	0	0
Juvenile 1	0.029	0.081	17	40	0	0
Juvenile 2	0.0116	0.0285	30	80	0	0
Juvenile 3	0.0023	0.0058	80	146	0	0
Juvenile 4	0.0016	0.004	105	185	0	0
Juvenile 5	0.0012	0.0032	110	220	0	0
Prerecruit	0.0006	0.0015	110	220	0	161
Early adult	0.0006	0.0015	190	570	286	489
Adult	0.0006	0.0022	400	920	730	1114
Late adult	0.0006	0.0022	1908	3473	1064	3123

Table 3 – Stage life history factor values of the Northern anchovy (Butler et al., 1993)

Stage	Daily mortality		Duration (days)		Daily fecundity	
	Min	Max	Min	Max	Min	Max
Egg	0.12	0.45	1.4	3.9	0	0
Yolk-sac larvae	0.19	0.59	1.4	3.9	0	0
Early larvae	0.187	0.345	8	23	0	0
Late larvae	0.047	0.087	35	71	0	0
Early juvenile	0.0009	0.017	45	100	0	0
Late juvenile	0.0029	0.053	60	138	0	0
Prerecruit	0.002	0.0037	200	632	0	19.4
Early adult	0.0011	0.0036	750	1250	199.2	230.7
Late adult	0.0011	0.0036	1000	1500	448.4	529.0

Each population s (s = sardine, anchovy and mackerel) evolves following a discrete stage-based dynamics given by:

$$\mathbf{n}^s_{i+1} = A^s \mathbf{n}^s_i, \quad i = 1, 2, ..., q \tag{14}$$

where the vector $\mathbf{n}^s_i$ describes the population at each stage i of life for species s. For sardines 14 stages are included in the model (Table 2), while for anchovies and mackerels 9 stages are considered (Tables 3 and 4). The transition matrix $\mathbf{A}^s$ is of the form (see Caswell, 1989):

$$\mathbf{A}^s = \begin{bmatrix} P^s_1 & F^s_2 & F^s_3 & \cdots & F^s_{q-1} & F^s_q \\ G^s_1 & P^s_2 & 0 & \cdots & 0 & 0 \\ 0 & G^s_2 & P^s_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & G^s_{q-1} & P^s_q \end{bmatrix}. \tag{15}$$

For each species s, F^s_i is the maternity per fish per unit time in stage i, P^s_i the probability of surviving in stage i and G^s_i is the probability of surviving in stage i and growing into the next stage. They are functions of the survival probability $p^s_i = e^{-Z^s_i}$:

$$P^s_i = p^s_i(1 - \gamma^s_i), \qquad G^s_i = p^s_i \gamma^s_i$$

where Z^s_i is the daily instantaneous mortality rate,

$$\gamma^s_i = \frac{(1 - p^s_i)p^s_i \exp(D^s_i - 1)}{1 - p^s_i \exp(D^s_i)}$$

and D^s_i is the duration within stage i. The evolution of each species is then completely described by the parameters F^s_i, Z^s_i and D^s_i.

As discussed in Zaldìvar et al. (1998) the model includes also density-dependent competitions between different stages of life, e.g. larval or juveniles intraspecific competitions (Matsuda et al., 1992). Fig. 8 schematically represents the complete evolution matrix **A** of the system with the three intercompetitive species. Each species is represented by its evolution matrix $\mathbf{A}^s$ and interspecific competitions are symbolized by grey cells.

The model contains 103 biological and physical uncertain factors, 72 describing the single species evolution (daily natural mortality (Z), duration (D) and daily fecundity (F) of sardines (I), anchovies (J) and mackerels (K)) and 31 accounting for migration and interspecific competitions (represented by lower case letters in Table 5). The lower and upper bounds of the distributions chosen for these factors can be found in the literature (see Smith et al., 1992; Butler et al., 1993; Dickerson et al., 1992, respectively, for sardines, anchovies and mackerels) and are listed in Tables 2–4. The output of interest in the model is the largest eigenvalue λ_{max} of the evolution matrix **A**, after 1-year simulation time. Since the number of input factors is high and the model is computationally expensive to run, a SA exercise using the Morris method (Morris, 1991; Saltelli et al., 2000a; Campolongo et al., 2006) is conducted (see also Zaldìvar et al., 1998) to screen non-influential factors in the model (factor fixing setting) with a conveniently small number of model evaluations.

Table 4 – Stage life history factor values of the chub mackerel (Dickerson et al., 1992)

Stage	Daily mortality		Duration (days)		Daily fecundity	
	Min	Max	Min	Max	Min	Max
Egg	0.126	1.614	16.43	21.14	0	0
Yolk-sac larvae	0.20	0.360	3.03	33.74	0	0
Early larvae	0.16	0.079	29.1	121.2	0	0
Late larvae	0.0009	0.055	20	144.5	0	0
Early juvenile	0.0009	0.045	17	289	0	0
Late juvenile	0.0016	0.045	45	144.5	0	0
Prerecruit	0.0005	0.0018	190	570	288.2	452.9
Early adult	0.0005	0.0018	400	920	691.7	1086.1
Late adult	0.0005	0.0018	1908	3473	1165.4	1831.4

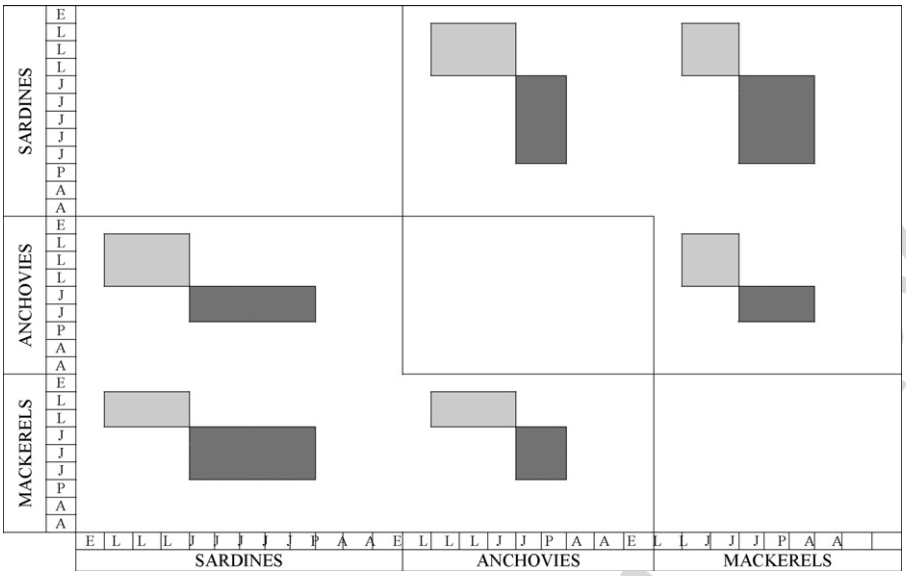

Fig. 8 – Schematic layout of matrix describing the evolution of the system with the three species of fishes. Grey cells represent the interspecies competitions, e.g. larval competition or juveniles competition. E indicates egg stage, L the larvae, J the juveniles, P the prerecruits and A indicates adults.

A short description of the method is offered here. In Morris, each input factor is allowed to vary over p levels and r trajectories are randomly generated. Each trajectory is built in such a way that factors are varied one-at-a-time across their levels. Along each trajectory, the so-called *elementary effect* of factor i, d_i, is evaluated as:

$$d_i(\mathbf{x}) = \frac{y(x_1, \ldots, x_{i-1}, x_i + \Delta, x_{i+1}, \ldots, x_k) - y(\mathbf{x})}{\Delta}$$

where Δ is a predetermined multiple of $1/(p-1)$, $\mathbf{x} = (x_1, x_2, \ldots, x_k)$ is a selected point in the trajectory and $(\mathbf{x} + e_i\Delta)$ is the transformed point where only the component i has been changed.

Table 5 – Results of SA by using the Morris method

Factor	μ	Factor	μ	Factor	μ	Factor	μ
DK5	4.3062	DJ4	0.1713	ZI9	0.0270	DJ9	0.0033
ZK5	2.2599	ZJ2	0.1685	ZI7	0.0259	aj12	0.0032
DJ3	0.9174	ZK7	0.1615	FI13	0.0222	aj23	0.0024
DK3	0.8679	ZK4	0.1571	ZK9	0.0205	DI13	0.0021
ZK1	0.8139	FJ8	0.1378	aj33	0.0198	B3	0.0018
DK2	0.7033	DI1	0.1370	DJ8	0.0180	al22	0.0016
ZJ4	0.6690	FJ7	0.1278	aj11	0.0172	aj21	0.0016
ZJ3	0.645	ZI3	0.1271	DI11	0.0172	al31	0.0008
ZJ6	0.6252	DI2	0.1132	DK8	0.0152	al12	0.0008
DK6	0.5572	DI6	0.0925	FI11	0.0123	D1a	0.0007
DJ7	0.5352	FK8	0.0872	FJ9	0.0123	D1b	0.0007
ZI4	0.5327	ZK6	0.0712	ZI13	0.012	al32	0.0006
DJ6	0.3715	ZK8	0.0678	D2b	0.0087	aj32	0.0005
ZK2	0.3439	DI9	0.0669	ZI10	0.0087	D2c	0.0004
ZJ5	0.2617	DI7	0.0637	al13	0.0076	D3a	0.0004
DJ2	0.2613	ZI2	0.0630	FK7	0.0063	al21	0.0003
ZJ1	0.2603	aj22	0.0599	FK9	0.0061	D3b	0.0002
DI3	0.2383	ZK3	0.0529	D2a	0.0054	D1d	0.0001
DK7	0.2314	ZI5	0.0528	DI12	0.0052	D3c	0.0001
ZJ8	0.2292	ZI6	0.0403	FI10	0.0049	D1c	0.0001
ZI1	0,2185	DI5	0.0368	FI12	0.0047	al23	0.0001
ZJ7	0.2050	DI10	0.0345	DK9	0.0045	al11	0.0001
DK1	0.1913	DI8	0.0339	b1	0.0043		
DI4	0.1880	ZI12	0.0328	b2	0.0041		
DK4	0.1877	ZI11	0.0327	aj13	0.0041		
DJ5	0.1854	ZI8	0.0310	al33	0.0037		
DJ1	0.1754	ZJ9	0.0300	aj31	0.0034		

Importance ranking of the 103 input factors.

The mean μ and the standard deviation σ of the absolute values of the elementary effects over the r trajectories are used as sensitivity measures to ascertain factors importance. μ measures the overall effect of a given factor on the output while σ accounts for all the effects of a factor that are non-linear or due to interactions with other factors (Morris, 1991; Campolongo et al., 2006). At first instance one may think of a parallel between σ and some combination of variance-based measures, e.g. $(ST_i - S_i)$. However, the two measures differ because of the curvature or higher order effects (i.e. the effects due to terms such as X^2, X^3, ..., and so on) that, while included in σ, are excluded from the difference $(ST_i - S_i)$ (Campolongo et al., 2006).

Morris can be considered as a global measure since it averages the effects of the factors at different points of the domain; it can also work with groups as shown in Campolongo et al. (2006). The computational cost of the Morris experiment is a linear function of the number of factors, $C = r(k + 1)$.

In the present experiment, each factor is varied across $p = 4$ levels, and $r = 10$ trajectories are generated, implying a total number of model evaluations $C = 1040$. Results of the application of the Morris method are shown in Fig. 9, which plots μ and σ for the 103 input factors. Each input factor with a high value of the estimated mean μ also presents a high value of the estimated standard deviation σ, highlighting that the model is strongly non-linear and non-additive. Fig. 9 shows two influential factors strongly separated from the others (DK5 and ZK5, respectively, duration and daily natural mortality of mackerels in the juvenile stage). A second group of factors is the one including duration of mackerels at larval and juvenile stages (DK2, DK3, DK6), duration of anchovies at larval and prerecruit stages (DJ3, DJ7), daily natural mortality of anchovies at larval and juvenile stages (ZJ3, ZJ4, ZJ6) and mortality of mackerels at the egg stage (ZK1).

Table 5 ranks the 103 factors according to decreasing values of the Morris measure μ. None of the factors involved in the migration and interspecific competitions appears in the first 30 factors identified by Morris; this means that these factors probably do not play a significant role in the magnitude of the population fluctuations. Moreover, it seems that the early stages of life affect more the output variability. In fact among the most 20 influential factors, only one (the mortality of early adult anchovies, ZJ8) is related with adult life, while two parameters connected to the prerecruit stage (DJ7 and DK7) are present. All the other factors are associated with juveniles or larvae stages. Finally, as we can see from Table 5, among the first 20 factors only 2 are related to sardines, namely ZI4 (ranked as 12) and DI3 (ranked as 18). It thus seems that the population dynamics is more influenced by the parameters describing anchovies and mackerels.

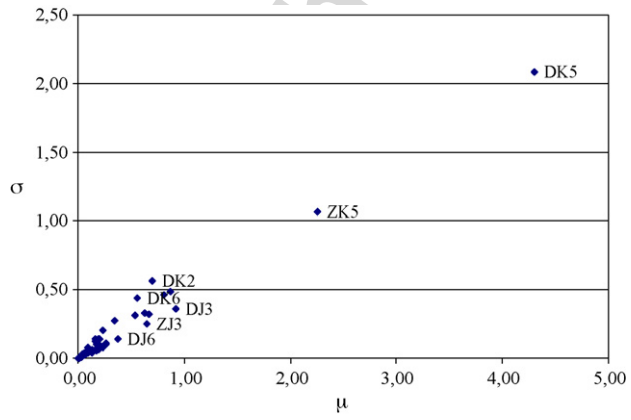

Fig. 9 – Result of the Morris experiment: scatterplot of the Morris σ vs. the Morris μ.

To confirm the results obtained by the Morris method, a SA on groups of factors applying variance-based techniques have been performed. The Sobol' method can in fact work with groups, since:

$$V(E(Y|\mathbf{u})) + V(E(Y|\mathbf{u}, \mathbf{v}) = V(Y) - V(E(Y|\mathbf{v}).$$

$V(E(Y|\mathbf{u}))$ and $V(E(Y|\mathbf{v}))$ are the first-order effects of groups $\mathbf{u}$ and $\mathbf{v}$, respectively, and they account for the contribution of all the factors belonging to each group plus the within-group interactions. $V(E(Y|\mathbf{u}, \mathbf{v}))$ estimates the effect of the interactions between the two groups.

With the aim of fixing the parameters describing the interspecific competitions and simplifying the model (factor fixing setting), the factors are divided into two groups. Specifically all the factors accounting for interspecific competitions are collected in a first group $\mathbf{v}$ while all the parameters describing single species evolution are put in a second group $\mathbf{u}$. The first and total order sensitivities indices are computed for both of them. The total number of model executions for this experiment is 4000 since (Eq. (12)) $k = 2$ and m is chosen to be 1000.

Results confirm that the set of factors describing the interspecies competitions do not affect the variance of the output. In fact more than 99.5% of the total outcome variability is imputable to the second group of factors. This exercise allows fixing the values of the 31 factors describing the interspecific competitions to their nominal values, obtaining a substantial simplification of the model.

Two other quantitative analyses on groups of factors using the Sobol' method have been performed on the remaining 72 parameters to confirm results obtained with the Morris method. First the variance of the output is apportioned to the contributions due to different stages of fish life, regardless of the species (see Table 6 for the grouping strategy). Finally, the decomposition of the variance grouping factors according to

Table 6 – Results of the SA experiment performed classifying the 72 factors into three groups

Groups	Factors	ST
Larvae	ZI(t), DI(t), $t = 1, \ldots, 4$ ZJ(t), DJ(t), $t = 1, \ldots, 4$ ZK(t), DK(t), $t = 1, \ldots, 4$	0.8567
Juveniles	ZI(t), DI(t), $t = 5, \ldots, 9$ ZJ(t), DJ(t), $t = 5, 6$ ZK(t), DK(t), $t = 5, 6$	0.3968
Adults	ZI(t), DI(t), FI(t), $t = 10, \ldots, 13$ ZJ(t), DJ(t), FJ(t), $t = 7, \ldots, 9$ ZK(t), DK(t), FK(t), $t = 7, \ldots, 9$	0.0835

The grouping strategy, based on age stage, and the total order sensitivity indices are reported.

species is estimated. In both cases the analysis is performed on three groups and the computational cost of each experiment is, according to (12), $C = 5000$ ($m = 1000$).

The second experiment, where factors are grouped by ages, supports the result obtained with the Morris method, according to which the parameters describing the adult stages do not influence the growth of the species. In fact the total order sensitivity index for the adult group is only 0.0835, while for juveniles and larvae the estimates are, respectively, 0.3968 and 0.8567. This allows concluding that, if the model under analysis is considered a good proxy of reality, from a fishing regulatory point of view the main effort has to be put on developing strategy for young species.

Also the last experiment, which groups parameters according to species, strengthens the screening results. The most important species is that of anchovies ($ST_j = 0.7334$), followed by mackerels ($ST_k = 0.2909$) and sardines ($ST_i = 0.0199$).

4. Conclusions

This work has shown how different sensitivity analysis methods can be applied to an ecological model. The choice of which method to use depends on various factors, such as the computational cost, the number of input factors and the setting for the analysis.

When the number of factors is low (i.e. less than 20) and the model is efficient, the best choice is to use variance-based methods, which provide more accurate sensitivity measures. In our first example based on the Lotka–Volterra equations, we showed that local measures are suitable only for linear models and provide the user with a measure dependent on the point of the inputs' domain chosen to estimate the derivatives. On the other hand the use of a regression analysis allows defining sensitivities measures (the squared standardized regression coefficients) which explore the entire input space. These measures are quantitative for linear models and can be used to rank factors also for moderately non-linear models. Moreover the model coefficient of determination can be used to detect the level of linearity of the model. However, when non-linearity or interactions account for a considerable fraction of the output variance, the standardized regression coefficient cannot be considered as a reliable sensitivity measure and the application of global techniques is advisable.

When the number of input factors is high (several tens or higher, as in the case of the fish population dynamics example) and/or the model is computationally expensive, the best way to reduce costs is to use a screening method such as Morris. This method is computationally cheaper, model free and can be used to identify non-influential factors (factor fixing setting). When the execution time of the model is very large, sensitivity analysis becomes problematic. In these cases, one may resort to analyst-time expensive approach such as automated differentiation (Grievank, 2000; Cacuci, 2003). In this case, the analyst may intervene on the code that implements the method, in order to efficiently compute a system of partial derivatives.

If the choice is instead driven by the setting of the analysis, first-order sensitivity indices are used for factor prioritization, while total indices or the method of Morris are the best choice for factors fixing setting. For factors mapping it is suggested to combine all these methods with Monte Carlo filtering, as shown in Saltelli et al. (2004).

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