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Qualitative modelling of ecological systems: Extending calculation procedures and applications

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"... any model that described the whole universe in detail would be much too complicated mathematically for us to be able to calculate exact predictions. One therefore has to make simplifying assumptions and approximations – and even then, the problem of extracting predictions remains a formidable one."

Stephen Hawking, *A Brief History of Time*, 1998

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Daniel Pereira,
November 2019,
Parma, Italy

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Paper 1 Daniel Pereira, Antonio Bodini, Marco Scotti (Manuscript) LevinsAnalysis: an R package for qualitative modelling.
Intended for Methods in Ecology an Evolution

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Intended for Community Ecology

Paper 3 Marco Scotti, Daniel Pereira, Antonio Bodini (Manuscript) Opportunities for the understanding of social-ecological systems using qualitative loop analysis.
Intended for Human Ecology Review (accepted with minor revision)

Summary

The aim of this Ph.D. was to contribute to the discipline of ecosystems networks, in particular to loop analysis, by improving on the current algorithm implementations, with particular emphasis in developing an approach to couple systems quantitative information to the analytical processes of loop analysis, and through it allow the exploration the mechanism behind a systems responsiveness to perturbations, that is, the importance of both the variables, the structure of linkages between them and the intensity of those linkages.

In this thesis, after a presentation of the loop analysis and its main drawback, the inherent lack of associated link intensity and the repercussions these have on the system's responsiveness, three chapters follow. In ***Chapter 3***, the *LevinsAnalysis R* package is presented. In this package the improved code and its applications explained and demonstrated through the application of the package functions to a case study, the *Savannah Fires* (Bodini & Clerici, 2016) model. This case was specifically selected to demonstrate the potential of the package and its novel approach to identification of the importance of linkage strength and path analysis. In ***Chapter 4***, I explore the Caspian Sea network prior to *Mnemiopsis leidyi* invasion, with the aim of investigating the mechanism behind the changes observed on multiple species and their importance compared with one another, the role that different species, the strength of interaction of the links and paths connecting them might have played in the system response to the different pressures it suffered. The result of this analysis, pointing to the importance of both kilkas and bony fish in the system's response to perturbations such as overfishing. Phytoplankton also emerges as potentially playing an important role in the system, in particular a possible negative input on this variable seems to be of importance in describing the changes observed in the system. From this chapter also comes about how the strength of interplay between variables and from there the strength of pathways connecting the system play a central role in the Caspian Sea system and its response to press perturbations. In ***Chapter 5***, a discussion is taken on the viability and potential use of loop analysis in the study of systems whose variables lay across the social and the ecological domains: species populations, predators and prey, but also governmental organizations, human dynamics and social mechanisms.

1. Introduction

1.1. Ecological Networks

Within any ecosystem, species and environment variables interact with each other in many and diverse ways. Predator-prey, parasite-host and competition are some of the examples of interactions between species that compose an interactive map that can be visualized as an ecological network. Through this network, species affect each other positively or negatively depending on the type of interactions between them. Species also affect each other indirectly through intermediate species. The net balance of the effect a species will have on each other thus depends on the strength of the interactions that connect them to each other but also on the distance between the species in the network.

Building and analysing an ecosystem network of interactions is a paramount task. Considerable time and effort are needed to uncover all the variables and interactions at work in the system, and from these all which play an important role in the system dynamics which should therefore be included in the network as essential to explain the behaviour of the system as a whole (Vacher et al., 2016). Network representations focus on certain aspects of the ecosystems. Perhaps the most famous network descriptions of ecological communities are the food webs (Cohen, 1978; Hall & Raffaelli, 1991; Pimm, 1982; Polis, 1991; Winemiller, 1990). They are complex architectures depicting who eats whom in ecosystems. They can be visualized as networks whose nodes represent species/ groups of species and the links between them the flow of energy associated to their trophic interaction. Their intricacy reveals that interdependence for food supply may extend across several trophic levels, connecting species that are far apart along the chain from producers to consumers. Food webs have been employed to understand mechanisms of ecological stability (Allesina & Tang, 2012; de Ruiter et al., 1995; MacArthur, 1955; Neutel et al., 2002), assess the ecological importance of species (Allesina & Pascual, 2009; Jordán, 2009; Jordán et al., 2008; Lai et al., 2012; O'Gorman et al., 2010) and understand mechanisms of secondary extinction (Allesina & Bodini, 2004; Dunne, Williams, & Martinez, 2002; Eklöf & Ebenman, 2006; Jordán, Scheuring, & Vida, 2002).

Networks as representations of ecosystems have been used to understand patterns of matter and energy circulations (Baird & Ulanowicz, 1989; Christian et al., 2009), ecosystem development and successional dynamics (Bodini et al., 2017; Scotti et al., 2009; R.E. Ulanowicz, 1986; Robert E Ulanowicz, 1980), effects of stress on ecosystems and ecosystem health (Bondavalli et al., 2006; Mageau et al. 1995; R.E. Ulanowicz & Mann, 1981) and environmental sustainability (Bodini et al., 2012; Pizzol et al., 2013).

Loop analysis, e.g., takes the description of the qualitative[1] state of relationships between variables in a system, that is, it considers the causal effect that a variable exerts on the rate of change of another. By its qualitative nature, loop analysis does not take into account the quantitative nature of the interactions between the individual variables.

Qualitative loop analysis translates the adjacency matrix of the interactions in an ecological community (Community Matrix, Levins, 1968) in a signed digraph. So, it translates an algorithm that is essentially based on the theory of systems of ordinary differential equations in a graphical algorithm that makes the analysis more intuitive and user friendly. Through graph and its analysis, it is possible to study important features of the networks structure, such as connectance, i.e., the number of interactions between species, path length, trophic levels and number of species per level and clustering. From the study of the structure of networks and the patterns that arise from it, further information can be taken from a system. Take loop analysis, from the application of its algorithm it's possible to study the mechanics of a systems evolution in response to alterations in the state of equilibrium of its component variables. That is, it allows the study of the system response to perturbations, both through how these perturbations affect each of the individual variables and the system as a whole, allowing then to understand the degree of importance that different variables, interactions and perturbations play in a system evolution. This knowledge can both be taken to study past events, to uncover the mechanics behind observed changes, or it can be applied as a predictive tool to understand the possible outcomes of present pressures in the systems.

Ecological networks are powerful tools to visualize and investigate systems mechanics, permeability and response to alterations on their state of equilibrium. Furthermore, the application of predictive analysis over networks where not only ecological variables are considered but also socio-economic (e.g., governmental organizations) makes ecological networks and their analysis an even greater tool in the organization, study and management of ecosystems.

1.2. State of the Art

Loop analysis is a method of qualitative modeling anticipated by Sewall Wright (1965) and systematically developed by Richard Levins, initially to study ecological communities. Despite its potential, since it was conceived loop analysis was not given the importance it deserved to be used in ecological investigations, mainly because quantitative models were the preferred tools in a framework in which the "anxiety for quantification" created a strong prejudice according to which "to know something we must define it precisely and measure it precisely" (Levins, 1970).

Several applications saw the light after the method was introduced: human physiology and disease (Levins, 1974); natural selection and fitness (Levins, 1975); phytoplankton-nutrient

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[1] When we make a "qualitative vs quantitative" distinction, we should bear in mind that the "qualitative" is also a quantitative in a technical sense, considering that having a binary "yes" or "no" entry depends on sampling and measurement errors and thresholds. So, being qualitative is a methodology, not philosophy.

relationships (P. Lane & Levins, 1977); populations genetics (Desharnais & Costantino, 1985); agriculture (Boucher et al., 1982); species interactions (Henry, 1980; Levine, 1980; Roughgarden, 1979; Vandermeer, 1981); acid deposition (Lane & Blouin, 1984, 1985); marine environment (Lane & Collins, 1985); in-lake enclosure experiments (Briand & Mccauley, 1978; Lane & Blouin, 1984). However, such applications appear as sporadic in the literature if confronted with other type of modelling, and a few groups used loop analysis systematically to clarify and understanding ecological dynamics. Attention to the method was promoted by researches that explored its theoretical foundations and tried to overcome its difficulties and limitations (Justus, 2006). The bulk of this work provided a reformulation of Levins' loop analysis for the qualitative modeling of complex dynamical systems (Dambacher et al., 2002; Dambacher et al., 2005; Dambacher et al., 1999; Dambacher et al., 2003). Progressively it had become clear that complexity was the central issue in environmental management, ecosystem ecology, and sustainability and tools to deal with such complexity were called for. In this framework new opportunities opened up for loop analysis and applications were directed to understand environmental issues in a multidisciplinary context (Bodini et al., 2000), to clarify cause and effects in ecological communities (Levins & Puccia, 1988; Levins & Schultz, 1996) and to tackle management questions (Ramsay and Veltman 2005).

Associated to the possibility to investigate complex systems that loop analysis offers the domain of its applications has become larger with the development of new research frameworks such as the Ecosystem Based Management (EBM) and the Socio-ecological systems (SES). These frameworks both emphasize the complex interactions that constitute the dynamics of the system of interest in which resources, actors, and governance systems interact to produce outcomes across these component parts. In particular these outcomes are the result of a series of feedback that buffer, amplify or even reverse the effects of actions imposed to the components so that often unintended effects emerge as outcomes of policies and management actions. Qualitative modeling approaches offer ways to assess these complex dynamics mediated by the feedbacks. Loop analysis in particular has revealed useful for examining and identifying potential outcomes from external perturbations and management interventions in data poor systems when very little is known about functional relationships and parameter values, which is the rule rather than the exception when variables across classical domains are included in the systems of interest (Babcock et al., 2016; Bell et al., 2015).

While the use of qualitative models for the study of complex systems has proven insightful, it nonetheless is difficult to apply to large or highly connected systems. This has been due, in part, to difficulty in the hand calculation of symbolic algorithms, but also to the interpretation of ambiguous results that arise in large complex systems. Recent computer software advances in symbolic processors, however, have eliminated the tedium of hand calculations. The present work contributed in this direction through the development of an *R* (R Core Team, 2019b) based software which has been conceived to deal with the most critical aspects of the algorithm complexity, such as the anatomy of the model so that the intricacy of the pathways is disentangled to highlight specific pathways and their role in spreading the effects of external perturbations; variation of interaction strength and their effects on variable response to external perturbations. In so doing that the functions of the package presented in this work present a theoretical advance in the treatment of model ambiguity, which is accompanied by a procedure which, based on a case study, illustrates how validation should be conducted exploiting data from real ecosystems.

1.3. Thesis aim and overview

This Ph.D. thesis aim was to contribute to the discipline of ecosystems networks, in particular loop analysis by improving on the current algorithm implementations, with particular emphasis in developing an approach to couple systems quantitative information to the analytical processes of loop analysis, and through it allow the exploration the mechanism behind a systems responsiveness to perturbations, that is, the importance of both the variables, the structure of linkages between them and the intensity the of those linkages.

The aims of this thesis are:

1) To improve on the loop analysis code made available by Bodini et. al., 2018, and develop an *R* package for a simple but comprehensive implementation of the qualitative modelling of loop analysis
2) To develop, within the *in-silica* application, an approach to explore the quantitative nature of networks within the loop analysis, that is, a method to explore the importance of strength and path information within a systems response to perturbations.
3) To uncover the mechanisms behind the changes observed in the Caspian Sea in the decades before *M. leidyi* invasion and the importance that the strength of different interactions and paths might have had in the systems response to the perturbations.
4) To explore the viability and potential of use of loop analysis in the study of socio-ecological system.

In this thesis, after a presentation of the loop analysis and its main drawback, the inherent lack of associated link intensity and the repercussions these have in the systems responsiveness, three chapters follow, which will ultimately serve as the basis of 3 papers. In ***Paper 1*** (***Chapter 3***), the *LevinsAnalysis R* package is presented. In this package the improved code and its applications explained and demonstrated through the application of the package functions to a case study, the *Savannah Fires* (Antonio Bodini & Clerici, 2016) model. This case was specifically selected to demonstrate potential of the package and is novel approach to identification of the importance of linkage strength and path analysis. In ***Paper 2*** (***Chapter 4***), I explore the Caspian Sea network prior to *M. leidyi* invasion, with the aim of investigating the mechanism behind the changes observed on multiple species and their importance compared with one another, the role that different species, the strength of interaction of the links and paths connecting them might have played in the system response to the different pressures it suffered. In **Paper 3** (***Chapter 5***), an exploration is made on the viability and potential of the use of loop analysis in the study of systems where not only ecological variables are included in the network but also human entities, such as governmental organizations, when compared to other qualitative modelling methodologies.

2. Methodology

2.1. Loop Analysis

Loop Analysis is a qualitative modelling technique that uses signed digraphs to represent networks of interacting variables (Richard Levins, 1974; Puccia & Levins, 1985). It allows prediction of the direction of change in the level (e.g. biomass, number of individuals) of system variables (single-species or group of species) in response to a parameter alteration or press perturbations on a targeted variable.

The loop analysis algorithm makes use of a specific kind of information, the qualitative state of relationship between two variables (their strength is not specified), that is, the typology of relationship between two variables (e.g., predator – prey) described through signed digraphs (or directed graphs), where a positive effect of species *i* on species *j* is represented by an arrow-headed link while a negative effect would be represented by a circle-headed link. The matrix counterpart of the signed digraph is the adjacency matrix, where the positive links are represented by a *+1* and the negative links by *-1*, while non-existing links between variables are represented with a *0*. Self-effects, e.g., as self-limiting growth rate are depicted in the adjacency matrix in the diagonal terms as -1, and in the signed digraph as circle-headed links connecting the variable to itself. Figure 2.1 the signed digraph, adjacency matrix is given for a simple system.

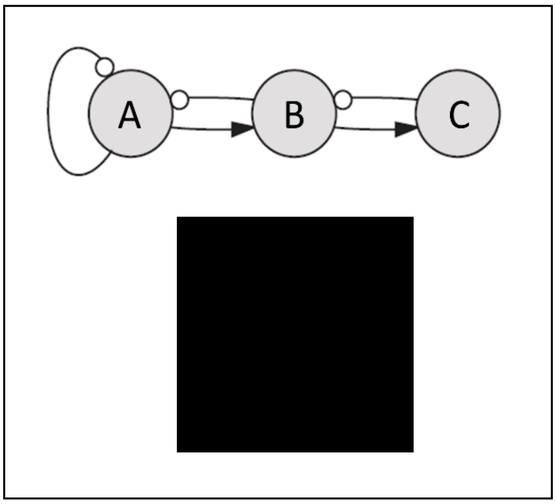

Figure 2.1: Signed digraph and corresponding adjacency matrix for a three trophic level linear chain. Values on adjacency matrix correspond to the qualitative effect of row variables in column variables

Press perturbations (Bender, Case, & Gilpin, 1984), are external inputs that affect the rate of change of a target variable with effects that propagate to the other species in the community and that are modulated by the feedback structure that is created by the multiple interactions among the variables. Their response can be predicted by the loop analysis algorithm and summarized in a *table of predictions* that becomes a diagnostic tool for the causes of change, where a prediction on whether the equilibrium value of a system variable is expected to increase, decrease or remain the same following the perturbation (Richard Levins, 1974). For any variable variations can be calculated by the loop formula.

$$\frac{\delta x_j}{\delta c} = \frac{\sum_{i,k}\left[\frac{\delta f_i}{\delta c}\right]\times\left[p_{ji}^{(k)}\right]\times\left[F_{n-k}^{(comp)}\right]}{F_n}$$

Where [$\partial f_i /\partial c$] expresses whether the rate of change of the target variables (i) increases or decreases because of the changing parameter (c); $[p_{ji}^{(k)}]$,is the pathway to the response variable from the target variable, $[F_{n-k}^{(comp)}]$ is the complementary feedback and $[F_n]$ is the overall feedback. Summation occurs along all paths from the target variable to the effect variable.

Path $[p_{ji}^{(k)}]$.

A path is a series of links connecting any two nodes in the system, without crossing any variable twice. Take the model from Figure 2.2. An example of a path would be that connecting the variables A and C, the three variable (*k*) path [A -> B -> C]. A positive input occurring on A (its rate of change increases,$\left[\frac{\partial f_i}{\partial c}\right] > 0$) would affect the state of equilibrium of C through this path, whose sign is given by the product of the signs of the links that form the path, in the case positive.

Circuits and Feedbacks.

A pathway that starts at one node and, by following the direction of links, returns to it without crossing any variable twice is called loop, or circuit. Any circuit produces a feedback that can be either positive or negative depending on the product of the signs of the links that form the loop. As there may be circuits of different length (with 1, 2, 3, ..., *k* variables involved), in a system there are as many levels of feedback as variables. Each level of feedback considers all the circuits (feedbacks) involving that particular number of variables. In the system of Figure 2.2 there are 3 levels of feedback. The first level of feedback comprises the only one variable circuit that is present in the system: the self-damping on variable A. Two resource-consumer interactions [A o-> B] and [B o-> C] produce two feedbacks of the second level, and the three variable feedback form the third level of feedback, which is created by two independent loops: the self-damping on variable A and the resource consumer interaction involving B and C.

Overall Feedback (*F_n*).

Overall feedback corresponds to the highest-level feedback of a system. It includes in it all the variables of the system, either combined in a single loop, or as part of disjoint loops including smaller subsets of variables, respecting that none is repeated twice. In the chain of three trophic levels depicted in Figure 2.2, the overall feedback corresponds to a third level of feedback (that is a feedback effect involving all the three variables). Because the three variables cannot be connected simultaneously in unique circuits, the overall feedback comprises the disjunct loops of A's self-damping and the resource consumer interaction between B and C that have a combined number of variables equal to 3. Its sign is obtained by multiplying the signs of the links involved, and this sign is further multiplied by(-1^{m+1}), where m is the number of disjunct loops entering the feedback. As the links involved are two negative and one positive, and there are two disjunct loops, the overall feedback is negative.

Complementary feedback (*F_{n-k}*).

The complementary feedback is the feedback that groups all the variables in the complementary subsystem, which is what remains from the system when the (k) variables in a path are excluded. In Figure 2 for a positive input on A and effect on B, the complementary subsystem is formed by C only. So, the maximum feedback can be a one variable feedback. But because C has no self-effect link, there will be a null (0) complementary feedback. Some axioms exist as follows: path from a variable to itself is equal to 1, while if all the variables are in the path (i.e., input to A and effect on C) there is no complementary subsystem, but the complementary feedback is equal to -1. These are two algebraic conveniences that are formally explained in Levins (1975) and Puccia and Levins (1985). Summation in the loop formula considers the fact that two variables can be connected by more than one path.

An identification of the elements and application of formula described above are provided in Figure 2.2.

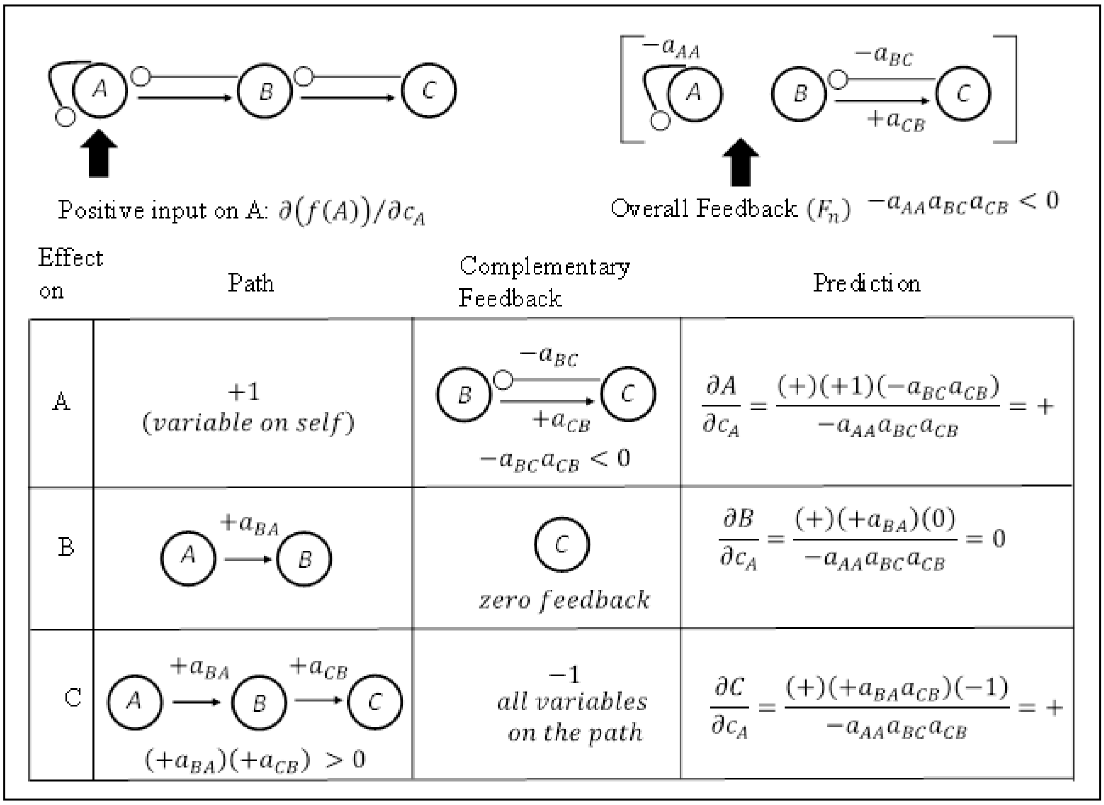

Figure 2.2: Signed-digraph of a three trophic level linear chain. Paths, complementary subsystems, and feedbacks used to calculate expected changes in the equilibrium level of the variables, in response to a positive input on A. The first term of the numerator in the formula under the Prediction header is the sign of the input (+).

2.1.1.Interaction Strength

From the analysis above to a simple three trophic level linear chain model it comes that there is a maximum of only one path connecting each variable, e.g. the only possible way to connect A to C would be [A -> B -> C]. When we consider a non-linear model, the number of paths between any variable can be different from 1. Take for example the model from figure 2.3. In this example between the variable A and variable D there are two possible paths, a longer path [A -> B -> C -o D] and a shorter path [A -> B -o D]. Both are negative and therefore the effect of A in D is negative.

Since calculations of the effect that an input in a variable as on another is the product of the sum of the effect carried through all its paths, it comes that with many variables and interactions the number of pathways between variables often increases, which leads to several null predictions. (i.e., the number of positive paths equals the number of negative paths).

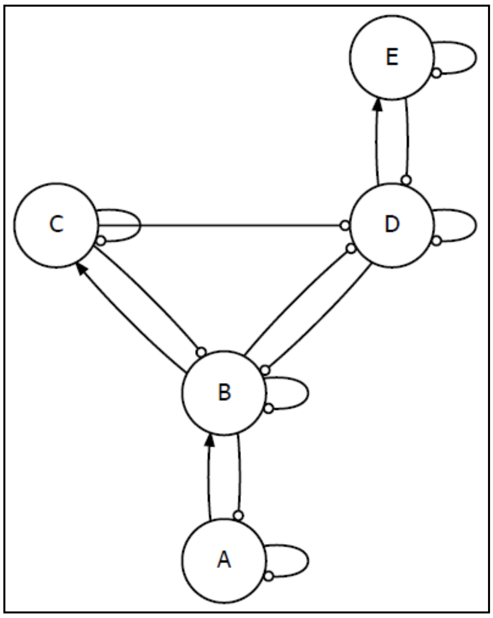

Figure 2.3: Signed digraph of a four trophic level non-linear chain model MM.

To solve such ambiguities a background quantitative simulation approach is adopted, which introduces a random assignment of the magnitude of each variable's interaction. During simulations the value of each link intensity is taken from a random distribution (e.g., uniform distribution) in the interval]0, 1]. After *n* simulations made over only those matrices that satisfied the conditions of stability an overall table of predictions is constructed by combining the *z* matrices that are stable (i.e. those with a determinant different than zero and admitting matrix inversion (Logofet, 1993)). For each of these matrices, unambiguous responses are generated in the table of predictions. The overall table of predictions is composed of symbols that depend on the percentages of signs from the various simulation runs. Therefore, if the same entry in the tables of predictions of all analysed matrices yields the same sign (+ or -) then the expected direction of change is unambiguous. However, there are cases where this is not true, and for which divergent predictions are computed. The conversion of signs from the simulations to the overall table of predictions depends on the percentages of positive (+) and negative (-) signs. The rules for sign assignment from simulations to overall table of predictions is summarized in Table 2.1.

[% of +] - [% of -]	Corresponding sign in the table
[-100, -50]	-
(-50, -20)	?- (tendency to -)
[-20, 20]	0*
(20, 50)	?+ (tendency to +)
[50, 100]	+
0 = 100%	0

Table 2.1: Rules to convert differences between percentages of signs obtained with simulations ([% of +] - [% of -]) into predictions (i.e. signs in the overall table of predictions). Round brackets indicate that the extremes are excluded; 0* is not a real zero, meaning no changes in the biomass/abundance of variables, but represents neutral result due to relatively balanced amounts of negative and positive effects. When after the complete set of simulations there are entries for which the absence of any effect was always recorded then the symbol in the overall table of predictions is 0, indicating proper absence of effect (see the last row of the table: 0 = 100%).

Due to the qualitative nature of loop analysis some information regarding the interaction between variables is lost. Namely the strength of their interactions. It comes then, that paths of the same length, regardless of the links that composed them, will always have the same strength and therefore the same importance in the sign determination. This leads to a detachment of the real-world interactions that a model may try to reflect, and in turn, the predictions from simulations may not match with the effects/trends observed in the real system. In a real system, variables interact with different intensities with each other, and therefore, the intensity of the effect of a path between any two variables won’t be a simple expression of the length of the path connecting them but both and expression of the length of the path and the strength of the links composing that path.

The importance and role that interaction strength between variables plays in the system response to perturbations is a problem that deserves attention. As presented in Paper 1, a formula was developed in order to allow for the exploration of this question.

By making use of the quantitative approach to solve the ambiguities from the existence of multiple pathway with opposite sign, a proxy to the real interaction strengths between variables can be generated. That is, by constraining the possible values of the real interaction strengths between variables to the interval]0, 1], and constraining the values of key entries in the adjacency matrix (instead of the randomly assigned values), one can, by proxy, simulate the real intensity of the interaction between any two variables.

The development of a proxy to the intensity of interaction between variables enables us to open new study possibilities on the ecosystems networks mechanics. As shown in Paper 1, by comparing the effect on predictions due to changes in the link strength of specific variables, and comparing those results with the default predictions (those using a uniform distribution to randomly assign strength values to links), and the trends for that ecosystem, it enables us to confirm or formulate hypothesis over the degree of interaction intensity that two variables might experience. As per Paper 2, by modulating the effect of all the pairs of interactions gradually and observing the level of change it causes too that when compared to the default prediction we can also have a glimpse into the level of importance that certain variables interactions might play in the systems response to perturbations. From here, and taken the opportunities provided by the code of the *LevinsAnalysis* package, we can now go further and explore the importance that paths may play. Prior to the possibility of modulating the interaction strength between variables, as noted above, paths strength was a result of their length. Now, with the opportunity to modulate the system to better reflect interactions intensity, there is the possibility to explore the true dimension of the paths strength and up to which point path length really is or not important for each individual system.

Even though the task at end might seem easy, it is still in fact a formidable one. It would be ill to suppose that with such a tool all the networks would yield all the information they have easily. In fact, as shown in Paper 2, this is far from the truth. Although some information can be retrieved from simple tests, a full in-depth knowledge of the system is necessary together with a long and laborious combing through of the data that can be retrieved from the simulations before conclusive answers can be made. But with time and patience, many hypotheses that remained unanswered can now be tested.

2.2. R Environment

In the age of informatics and *in-silica* experiments, the performance of statistical analysis too needs a place. The open source *R* environment (R Core Team, 2019b) is such a place.

R is an open source language and environment (based on *S* language (Chambers, 1998)) for statistical computing and graphics (R Core Team, 2019b). It provides a wide variety of statistical and graphical techniques, allowing for easy data handling, calculations and display of publication quality plots. Although a great care has been taken over the defaults for the statistical bases provided, one of the mains strength of *R* language and its environment is its versatility, by allowing not only the user to manipulate and explore the potential of each of the functions provided directly with the basic installation and the vast array of others provided in the its vast library CRAN (R Core Team, 2019a, 2019b) in the form of packages, but also by allowing the users to generate new functions and packages for answer to particular questions he may find, and to be able to share those new implementations with others and thus contribute to the ever expanding *R* repository.

As shown in ***Chapter 3*** and further explored in ***Chapter 4***, the *R* environment proves to be a useful tool when at end is a task for generation of new statistical analysis, by both proving its great flexibility and easy access and use.

3. A package for Loop analysis: "*LevinsAnalysis*"

LevinsAnalysis: An R package for qualitative modelling

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3.1. Summary

1) Loop analysis is a qualitative modelling technique that uses signed digraphs of interacting variables, and allows the prediction of the direction of change in the biomass of system variables in response to parameter alteration targeted to specific variables

2) Here, we introduce *LevinsAnalysis*, an *R* package for loop analysis. The functions put forward within this package allow the user to exploit the full potential of the qualitative algorithm of loop analysis coupled with a novel approach to explore the importance of interaction strength and path analysis, keeping the drawbacks of the qualitative nature of the analysis at a minimum.

3) In addition to an overview of the package a practical application of the package is made, highlighting its novel approach to systems mechanics study.

Keywords: Levins loop analysis, graph structure, community matrix, predictions, complex systems, open-source software

3.2. Introduction

Loop analysis is a qualitative modelling technique that uses signed digraphs to represent networks of interacting variables (Richard Levins, 1974; Puccia & Levins, 1985). Loop analysis allows predicting the direction of change in the level (e.g. biomass, number of individuals) of system variables in response press perturbations. These latter are factors (both internal and external to the system) that alter the parameters in the rate of change of the variables so that these functions increase or decrease with effects on the level of the affected variable. Also, there are effects beyond the target variable: impacts cascade through the entire community using pathways of interactions and are modulated by the feedback structure that is created by the reticulate connections among the variables. The loop analysis algorithm predicts those changes and summarizes them in a *table of predictions* that becomes a diagnostic tool for the causes of change. Being the algorithm qualitative, the predictions indicate only the direction of change in the equilibrium level of the variables: increase (+), decrease (-) or no change (0).

An increase in the number of variables and/or interactions raises the chance of having multiple pathways with opposite effects. In these cases, the algorithm might yield ambiguous results, with positive and negative pathways that act in opposite directions. In these cases, there can be a prevalence of either positive effects or negative effects but also compensation: in any case in the absence of any quantitative specification for the link magnitude it remains impossible to precisely define the final outcome. To overcome this difficulty a numerical simulation routine can be helpful. In general, this routine keeps the community structure fixed and the interaction coefficients are randomly assigned. Coupling the algorithm with the simulation allows for solving ambiguous predictions or at least finding a tendency for change, whereas a complete balance of positive and negative effects is meant as compensation of effects that results in no change in the predicted level of that variable. Such possibility allows the user to recreate a step closer the real-world interactions.

The *LevinsAnalysis R* package is a collection of functions developed with the aim to exploit the full potential of the qualitative algorithm of loop analysis keeping the drawbacks of the qualitative nature of the analysis at a minimum. With this package the user can explore in depth the effects of inputs that enter the system through any of the variables that compose it. Single input as well as concurrent inputs, that is contemporary inputs on more than one component, can be analysed using interaction strengths assigned to the links. The package is designed to help the user to investigate 1) the causal mechanisms behind changes in the biomass level of species in an ecological network, through unveiling the relationships between the sources of change (i.e., the pressures), the structure of the linkage between the variables, and the variation in the level of the variables.

In this paper, we present an overview of *LevinsAnalysis* highlighting some of its functionalities and advantages in comparison to other existing loop analysis algorithms. An in-depth analysis of loop analysis algorithm, its uses and interpretation go beyond the scope of this paper. Nevertheless, interested users are recommended a selection of papers (Bodini, 1998, 2000; Levins, 1974; Puccia & Levins, 1985). For a more comprehensive description of the package *LevinsAnalysis* functions, consult the in-package *help.pages* of each function, where a more detailed description of each function can be obtained along with fully functional examples.

3.3. *LevinsAnalysis*

3.3.1. Overview

The *LevinsAnalysis R* package is designed to allow exploring the structure of a network, generating signed digraphs, simulating the effect of press perturbations, with the novel option to manipulate the intensity of interactions between variables in an inherently qualitative algorithm.

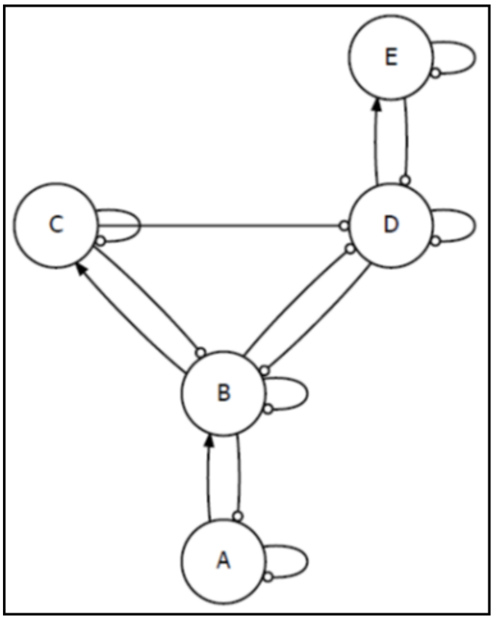
In brief, the package's functions performs the following: 1) structural information of the network (i.e., network stability status, number of variables, number of links between variables, number of simple paths and their information); 2) graphical visualizations of the network through signed digraphs; 3) table of predictions for single and concurrent inputs using either random or user defined interaction strengths for network links. In Table 3.1 a summary of each function present in the package with brief description of their use.

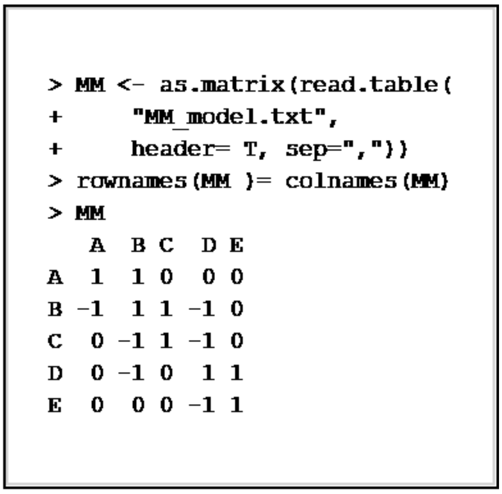
Below we will describe in more details the type of data necessary to run the various functionalities in *LevinsAnalysis R* package. A practical example of usage will be given afterwards using one of the model's that the package makes available as case studies.

3.3.2. Data Requirements and Input

Different functions from the package *LevinsAnalysis* use different types of data for input, and apart from the original adjacency matrix describing the Ecological Network to be studied, all the other data matrices can be obtained from within the package through the computation of dedicated functions. Independently from which data type it is all data matrices used by the package are formatted in the same manner, and therefore, can be imported using the same code. For the sake of simplicity, here we describe how to import a community matrix into the *LevinsAnalysis* package.

The loop analysis algorithm exploits the qualitative character of the interactions between any two variables and translates this information into a signed digraph made of only two types of connections: arrows for positive qualitative effects and circle-head links for qualitative negative effects. The matrix counterpart of the signed digraph is the adjacency matrix, where the positive links are represented by a +1 and the negative links by -1, while non-existing links between variables are represented with a 0. In Figure 3.1 a representation of a signed digraph for an example model (model MM) is given.





```
> MM <- as.matrix(read.table(
+      "MM_model.txt",
+      header= T, sep=","))
> rownames(MM )= colnames(MM)
> MM
   A  B C  D E
A  1  1 0  0 0
B -1  1 1 -1 0
C  0 -1 1 -1 0
D  0 -1 0  1 1
E  0  0 0 -1 1
```

Figure 3.1: Model MM signed digraph. In the graph (on the left), positive interactions are denoted with arrow-headed links while negative interactions are visualized with circle-headed links. Code script to load an adjacency matrix from a txt file (on the right). In the original txt file, the first line consists of the names of each node. Each subsequent row indicates the effect of each variable *i* on each variable *j* following the order of variables on the first line.

For the use of the *LevinsAnalysis* package, an adjacency matrix (symmetrical matrix) is necessary, constructed using the appropriate symbology indicated above and written by indicating the qualitative direct causal effect from variable *i* (row) on variable *j* (column). Column and row variables should be identified. Figure 3.1 reports the code needed for loading the adjacency matrix for the MM signed digraphs. This example model serves to demonstrate how an adjacency matrix should look like.

3.3.3. Visualization

Visualization of a signed digraph is always a useful tool to better understand the interplay between nodes. In *LevinsAnalysis R* package the user has the possibility to graphically represent both the community matrix and the table of predictions in the form of signed digraphs. The function `cm_graph` allows computing the community matrix, allowing the user to quickly visualize its corresponding network as signed digraph. The function `pred_graph` allows the user to compute the results from the table of predictions, i.e., the predicted effect in a variable *j* (column; arrows end) due to a press perturbation in an input in variable *i* (row; arrow begin) as obtained from the simulations, giving the user a supplementary tool to observe and study the effects that a press perturbation might have in the network (example signed digraph in ***Annex A: Pred_graph***). The code for generation of either of the signed digraphs can be seen in the *help.page* of each of the functions, here functional examples codes are available using in package models, such has the *Savannah Fires* model from Bodini and Clerici (2016) which we will use bellow as an example application of the package.

3.3.4. Algorithm overview

The analytical functions available in the LevinsAnalysis package can be divided in three categories, the graphical (already discussed above), the structural and the predictive functions. In Table 3.1 we present the functions of the package together with a brief indication of their use.

The structural functions are intended to provide the user with an in-depth knowledge of the network structure and level of interaction between variables, and so unravel and study hypothesis on how certain pressures might affect the system through the study of the networks interconnectedness. The structural functions provide information about the following network features: number of nodes, number of links between variables, total number of simple paths, and a description of each simple-path present in the system (variables involved, path length, its sign and strength), trophic level of each variable and if the adjacency matrix of the network is stable.

The core functions for the loop analysis are in the predictive group. With `levins_predictions` the user is able to run simulations for the effect of inputs for any variable so that a series of predictions upon any single variable of the model is obtained; simulating input to each variable one obtains the so called table of predictions, that is a summary of all the possible consequences on the level of each and every variable due to input on any single component. The routine `levins_concurrent` allows simulating the effect of more than one input at a time (concurrent inputs). Advancing on existing methodologies, the approach used in our algorithm solves the problem of uncertain results due to the existence of multiple paths with opposite signs. In our algorithm strength values are assigned to each of the links between the nodes within the interval]0,1] using one of three predefined types of distributions: uniform, normal and pareto, which can be selected by the user. An option that allows the user to select the strength values for a more reliable description of the system is also at disposal. Although some uncertain results may still be obtained (signed as 0*), the user is now able to distinguish between true null effects and between 0 net effects where the actual effect, that is, results for which there is a balance between the strength of positive and negative paths on the variable. A last function that completes the predictive functions is `pred_correlation` which allows investigating whether correlations emerge from the predictions.

Graphical Functions	**Description**
`cm_graph`	Generates signed digraphs from adjacency matrix
`pred_graph`	Generates signed digraphs from table of predictions
Structural Functions	**Description**
`cm_interaction`	Calculates the number of paths beginning in row variables and ending in column variables
`cm_paths`	Retrieves the information for all simple paths
`cm_stability`	Tests the adjacency matrix stability
`cm_strength`	Generates a table of interaction strength
`cm_structure`	Retrieves structural information
Predictive Functions	**Description**
`levins_predictions`	Calculates the table of predictions for single inputs
`levins_concurrent`	Calculates the table of predictions for concurrent inputs
`pred_correlation`	Calculates the level of correlation between predictions

Table 3.1: Functions present in *LevinsAnalysis R* package

3.3.5. Example Application

Given an ecological network model, to use the loop analysis algorithm present in the *LevinsAnalysis* package and compute a prediction table is a straightforward process. Here follows a brief sketch of the functionalities included in the package. They refer to the following issues: 1) testing for model stability, 2) graphical representation, 3) structural information, 4) computing a strength matrix 5) highlighting simple paths, and 6) computing a table of predictions. A quick analysis and discussion of the results will be performed to interpret the analytical output. In the ***Annex A: R Code for Simulation*** follows the script used for the analysis performed.

The model to be used in this practical example, called here *Savannah Fires* (Antonio Bodini & Clerici, 2016), is already loaded with the package, therefore a simple call for its tag name (as shown in Table 3.2) will produce the adjacency matrix. The graph related to this example is depicted in Figure 3.2.

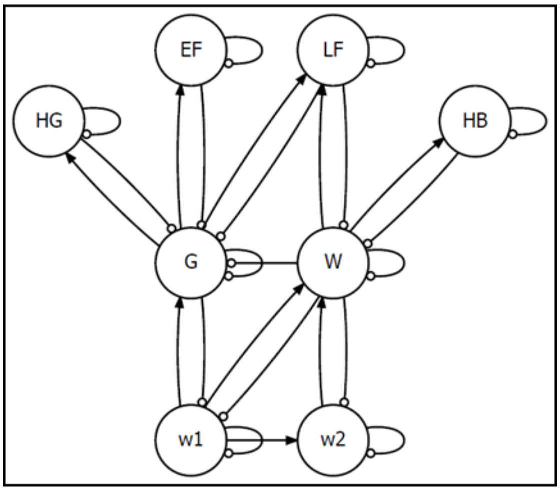


Figure 3.2: Savannah Fires model (Bodini and Clerici, 2016) signed digraph. Keys for nodes: w1 – superficial water table; w2 – deep water table; G – grasses; W – woody plants; HG – grazers; HB – browsers; EF – early fires; LF – late fires.

The interest in the study of this model is to test the hypothesis found across the literature for the type of interaction between two nodes, *G* (grasses) and *W* (woody plants). In particular, there would be a competitive interaction in savannah ecosystems between grass and woody vegetation that may affect the dynamics of this system. Bi-stability was documented for these systems, with possible dominance of either grass (G) or woody (W) in different conditions. In their paper, Bodini and Clerici (2016) tested whether the reciprocal inhibition between grass and woody vegetation could affect and in what form the dynamics of the savannah system. These authors highlighted that a model that reproduces in a correct way experimental data is one in which only one inhibition link from W to G, [*W -o G*], characterizes the interactions between the two vegetation variables. Here we show how by means of the *LevinsAnalysis* package one can explore in detail the effects of this link when its magnitude varies. For that we will generate strength matrices where we define the strength of interaction of the pair W-G and compare predictions obtained with those of a purely randomly generated strength matrix. A first test in the analysis of our function is always to test its stability, this is done by running the adjacency matrix through the function `cm_stability`. The model is a stable matrix, and so no reworking is needed. One can proceed to the second step which will generate the signed digraph. In the example code provided in Figure 3.3 we demonstrate how a user-defined structure for the graphic generation (Figure 3.2) can be constructed using the `cm_graph` function.

```
> savannah_coord <- cbind(c(2,3,2,3,1,4,2,3),
+     c(0.75,0.75,2,2,3,3,3.5,3.5))
> colnames(savannah_coord) <- c("x", "y")
> rownames(savannah_coord) <- c("w1","w2","G",
+     "W","HG","HB","EF","LF")
> cm_graph(savannah_fires, fname = "savannah_fires",
+     layout_g = "user", coord = savannah_coord,
+     save_file = "pdf")
```

Figure 3.3: *R* Code script for generation of a signed digraph for the model Savannah Fires (Bodini and Clerici, 2016) using a user-defined node layout on LevinsAnalysis graphical function cm_paths. Keys for nodes: w1 – superficial water table; w2 – deep water table; G – grasses; W – woody plants; HG – grazers; HB – browsers; EF – early fires; LF – late fires.

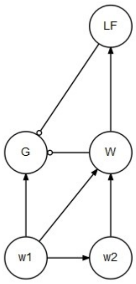
After the graph is obtained the following step in the analysis is to describe the structure of the model. The `cm_structure` function does this. The structural analysis tells that the model is not very intricate with its 160 simple paths, a result of 26 links, 8 of which are self-loops and therefore do not count for simple paths construction.

The package capability to define the values of interaction strength between variables was applied to the savannah model to understand the effect of varying the magnitude of the link [*W -o G*]. The function `cm_strength` makes this computation. Three scenarios were defined as follows: i) the interaction strength for the *W-G* pair is limited to the interval [0.5, 1], which will emulate a high intensity interaction, ii) the interaction strength for the *W-G* pair is limited to the interval]0, 0.5], which will emulate a low intensity interaction, iii) the interaction strength for the *W-G* pair is defined randomly using a uniform distribution, with the value falling in-between those of the two scenarios. After we compute the strength matrices, we can retrieve the information of all simple paths for each of the scenarios. The appropriate function is `cm_paths` which renders the full list of simple paths or specific subsets. In the case of the savannah model of Figure 3.2 we considered here only the paths linking variable w1 (superficial water table, see Figure 3.2 for details about the keys for the variables) to *G*. The results of this function are always exported to a *txt* file and shown in Figure 3.4.

a

nodes	path strength	# nodes	path sign
w1, w2, W, G	0.124122591	4	-1
w1, w2, W, LF, G	0.06332306	5	-1
w1, G	0.502281337	2	1
w1, W, G	0.244773276	3	-1
w1, W, LF, G	0.124874873	4	-1

d



b

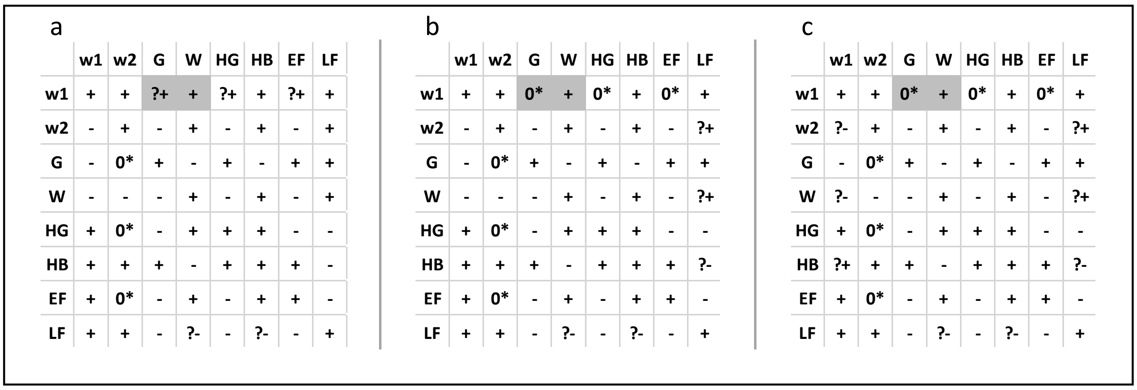
nodes	path strength	# nodes	path sign
w1, w2, W, G	0.064016084	4	-1
w1, w2, W, LF, G	0.062821555	5	-1
w1, G	0.500270659	2	1
w1, W, G	0.126248062	3	-1
w1, W, LF, G	0.123892295	4	-1

c

nodes	path strength	# nodes	path sign
w1, w2, W, G	0.186271793	4	-1
w1, w2, W, LF, G	0.062768681	5	-1
w1, G	0.501167574	2	1
w1, W, G	0.365914794	3	-1
w1, W, LF, G	0.123303634	4	-1

Figure 3.4: Information for paths between w1 and G, with a) randomly assigned strength values, b) strength values defined to emulate a low intensity interaction between W-G, c) strength values defined to emulate a high intensity interaction between W-G. Graph d) designed to include only the links leading from w1 to G.

After the analysis of the structure of our model we proceeded to the loop analysis proper. Simulating press perturbations on each of the variables of the system the function `levins_prediction` renders a table of predictions for the level of the variables. Three simulations were run for each of the interaction strengths scenarios described above. The tables of predictions from our runs are show in Figure 3.5 (key for each symbol used in the table of predictions and table of concurrent predictions are shown and explained in ***Chapter 2: 2.1.2 Interaction Strength***).



a

	w1	w2	G	W	HG	HB	EF	LF
w1	+	+	?+	+	?+	+	?+	+
w2	-	+	-	+	-	+	-	+
G	-	0*	+	-	+	-	+	+
W	-	-	-	+	-	+	-	+
HG	+	0*	-	+	+	+	-	-
HB	+	+	+	-	+	+	+	-
EF	+	0*	-	+	-	+	+	-
LF	+	+	-	?-	-	?-	-	+

b

	w1	w2	G	W	HG	HB	EF	LF
w1	+	+	0*	+	0*	+	0*	+
w2	-	+	-	+	-	+	-	?+
G	-	0*	+	-	+	-	+	+
W	-	-	-	+	-	+	-	?+
HG	+	0*	-	+	+	+	-	-
HB	+	+	+	-	+	+	+	?-
EF	+	0*	-	+	-	+	+	-
LF	+	+	-	?-	-	?-	-	+

c

	w1	w2	G	W	HG	HB	EF	LF
w1	+	+	0*	+	0*	+	0*	+
w2	?-	+	-	+	-	+	-	?+
G	-	0*	+	-	+	-	+	+
W	?-	-	-	+	-	+	-	?+
HG	+	0*	-	+	+	+	-	-
HB	?+	+	+	-	+	+	+	?-
EF	+	0*	-	+	-	+	+	-
LF	+	+	-	?-	-	?-	-	+

Figure 3.5: Table of predictions for the Savannah Fires model (Bodini and Clerici, 2016), following three interaction strength scenarios for the link W -o G. a) strength value set to emulate a low intensity interaction, b) value randomly assigned following a uniform distribution, c) strength value set to emulate a high intensity interaction. Predictions marked in grey are those for which there is an interest in analysis. Keys for nodes: w1 – superficial water table; w2 – deep water table; G – grasses; W – woody plants; HG – grazers; HB – browsers; EF – early fires; LF – late fires.

The scenarios for predictions (Figure 3.5) would be confronted with evidences from the literature. It comes from the analysis of the literature that an increase is expected in the level of woody plants (*W*) when there is an excess in the precipitation levels, which clearly corresponds to a positive input on the superficial water table (*w1*). Looking at the first row of each table, we can see the predicted direction of change in the level of the column variables due to a positive input on *w1*. By comparing the predicted effects on *G* and *W* (marked as grey) we can see that the only alternative scenario that matches with the original table of predictions (Figure 3.5-b), and the trends described in the literature, is that of Figure 3.5-c, which describes a system where the intensity of interaction between *W-G* is on the high spectrum.

A quick look at the lists of paths information retrieved previously for each scenario allows us to have a glimpse at how this single alteration of a strength value was able to produce different results. Figure 3.4-a:c summarizes the information for the paths between *w1* and *G*, which are depicted in a graph (Figure 3.4-d) As many as 5 simple paths connect *w1* to *G*, and only two of these paths include a direct link from W to G (Figure 3.4-a,c). By comparing the scenario results a change in predictions comes passing from the low intensity scenario (low strength for the link [*W -o G*]) to the other two scenarios. In the first case a positive input to w1 is expected to increase both W and G which would not explain the dominance of woody vegetation in the case of heavy rain, as documented in the literature. The high interaction scenario (Figure 3.4-c, 3.5-c) seems ecologically more realistic so that it introduces the hypothesis that for the phenomenon of woody dominance in case of excess rain a strong inhibitory effect of W over G is necessary.

Further analysis of the effect of the intensity of the interaction strength between *W* and *G* could be done to pinpoint the exact level at which the predictions would still fit with the observed trends. Another analysis possible by the *LevinsAnalysis* package would be to compute the effect of multiple concurrent inputs on the system and cross check these predictions with observed trends, but this analysis and further ones are beyond the scope of our analysis here. A more thorough use of each function can be seen on each functions *help.page*.

3.3.6.Extras features

To facilitate the understanding and use of the functions available in the *LevinsAnalysis* package we include example data matrices of each of the different types of data used within, all based on a simple 5x5 imaginary ecological network model (model MM from Figure 3.1) designed for simple use and understanding of the outcomes that can be expected. A small data library was also added to the package, composed of 4 different models, each representing a real-world ecological network system which have been studied using the loop analysis methodology. These extra features are presented and briefly described in Table 3.2.

Example Data	**Description**
`MM`	Adjacency matrix for example model MM
`PM`	Table of Predictions for example model MM
`P_Pred`	Matrix of positive percentage predictions for model MM
`SM`	Interaction strength matrix for model MM
Example Models	**Description**
`baja_california`	Adjacency matrix for the Baja California ecological network (Martone, Bodini, & Micheli, 2017)
`black_sea`	Adjacency matrix for the Black Sea ecological network (Antonio Bodini, Rocchi, & Scotti, 2018)
`lake_mosvatn`	Adjacency matrix for the Lake Mosvatn ecological network (Antonio Bodini, 2000)
`savannah_fires`	Adjacency matrix for the Savannah Fires ecological network (Antonio Bodini & Clerici, 2016)

Table 3.2: Data Library from LevinsAnalysis. Example model MM and matrices for function testing, and real-world ecological network models.

3.4. Conclusion and future developments

The value features that the *LevinsAnalysis* package brings in comparison to other existing analytical tools of loop analysis in ecological systems (and to some extent the code used and made available by Bodini and Clerici, 2016) are i) the use of a quantitative approach (here designated has interaction strength) to deal with the ambiguities in the predictions by allowing the user to specify the strength of particular variable pairs, ii) the retrieval of descriptive information of each path, and iii) allowing the user to compute the effect of concurrent predictions, basing the predictions on the same theoretical background as used for single inputs, instead of the use of simple arithmetic calculation over the signs of predictions of single inputs.

Although the loop analysis is a qualitative approach, coupling it with a quantitative methodology to deal with the effect of multiple paths with opposite effect may help disentangling the effects of intricate paths that would otherwise cloud the real effect of an input. This methodology takes in consideration the effect that the intensity of interactions between nodes, and the length of the paths between two variables affects the effect an input will ultimately have. This approach allows also the users to manipulate the strengths of each variable pair to make the system more ecologically reliable in describing real cases and to study the effect of how the strength of the links can influence the response of the system to press perturbations. Coupled with paths information function, it enables the user also to study in detail how a change in the value of a given interaction strength will affect the strength of paths that connect any two variables and how this will possibly affect the modelling outcome.

The *LevinsAnalysis* is continuously developing. Debugging to make it more efficient in its computations and implementation of in-function error message system to allow the user to better understand where a problem in case of a malfunction is are one of the branches of this continuous upgrade on the package. Another branch of this upgrade is the introduction of new functions to 1) test the models validity, relying not only in mathematical data, but testing the model directly versus the real world ecosystem which emulates, and 2) functions which will allow the user the further explore its network mechanics and interpret the results from the loop analysis predictions it might produce.

In conclusion, the *LevinsAnalysis* has been designed to facilitate the use, integration and interpretation of the loop analysis methodology in a user's network analysis protocol. The functions here included have the intention to give the user a tool to study and get a more comprehensive understanding of the mechanics of his network in their response to perturbations, and the importance that certain variables and paths might play in this response. The use of loop analysis in the study of ecological networks is a growing field, and we look forward to seeing new discoveries made through the use of *LevinsAnalysis*.

3.5. Annex A – Supplementary materials

3.5.1.Pred_graph

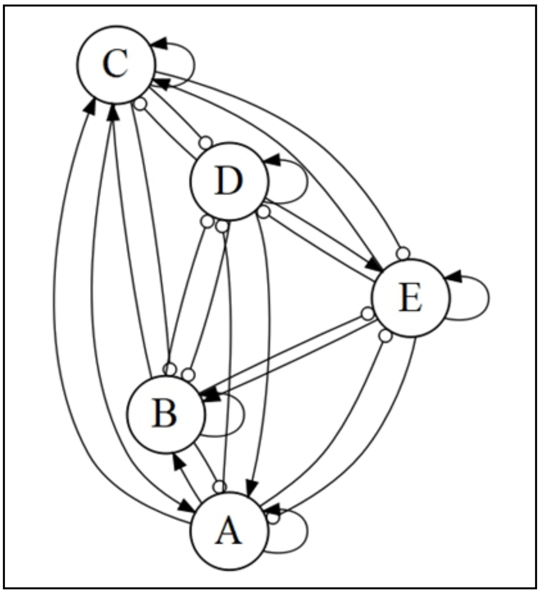


Figure 3.6: Signed digraph from table of predictions for the example model MM. Arrow-headed links represent positive effects and circle-headed links represent negative effects. More information on the use of the pred_graph function can be found on the functions *help.page*

3.5.2.R code for simulations

Bellow follows the R code used for the simulations discussed in this chapter. For brevity, only selected results of the executed functions are shown.

```
> # loading of LevinsAnalysis package
>library(LevinsAnalysis)
> # visualization of the models adjacency matrix
> savannah_fires
   w1 w2  G  W HG HB EF LF
w1 -1  1  1  1  0  0  0  0
w2  0 -1  0  1  0  0  0  0
G  -1  0 -1  0  1  0  1  1
W  -1 -1 -1 -1  0  1  0  1
HG  0  0 -1  0 -1  0  0  0
HB  0  0  0 -1  0 -1  0  0
EF  0  0 -1  0  0  0 -1  0
LF  0  0 -1 -1  0  0  0 -1
> # stability test
> cm_stability(savannah_fires)
[1] "The community matrix is stable"
```

```
> # data structure extraction
> cm_structure(savannah_fires, fname = "savannah_fires")
...
No. of Nodes of the Community Matrix: 8
Total no. of Nodal Interactions: 26
Number of possible paths of the Community Matrix: 160
...
> # creation of interval matrices for interaction strength
> savannah_minv <- matrix(rep(0,(length(savannah_fires))), nrow =
sqrt(length(savannah_fires)))
> row.names(savannah_minv)=colnames(savannah_fires)
> colnames(savannah_minv)=colnames(savannah_fires)
> savannah_maxv <- matrix(rep(0,(length(savannah_fires))), nrow =
sqrt(length(savannah_fires)))
> row.names(savannah_maxv)=colnames(savannah_fires)
> colnames(savannah_maxv)=colnames(savannah_fires)
> # value assignment for interaction strength intervals
> savannah_minv[4,3]= c(0.5)
> savannah_maxv[4,3]= c(0.5)
> # generation of strength matrix
> savannah_strg <- cm_strength(savannah_fires, fname = "savannah_fires")
...
> # generation of strength matrices with user defined intervals for interaction
strength
> savannah_strg_min <- cm_strength(savannah_fires, INT_MIN = savannah_minv, fname
= "savannah_fires_min")
...
> savannah_strg_max <- cm_strength(savannah_fires, INT_MAX = savannah_maxv, fname
= "savannah_fires_max")
...
> #retrieval of path information
> NodetN <- c("w1","G")
> cm_paths(savannah_fires, savannah_strg$`Average Strength Matrix`, Threshold =
"NodetN", fname = "savannah_fires_w1_g")
> cm_paths(savannah_fires, savannah_strg_min$`Average Strength Matrix`, Threshold
= "NodetN", fname = "savannah_fires_min_w1_g")
> cm_paths(savannah_fires, savannah_strg_max$`Average Strength Matrix`, Threshold
= "NodetN", fname = "savannah_fires_max_w1_g")
> # computation of levins analysis algorithm
> savannah_lp <- levins_predictions(savannah_fires, fname = "savannah_fires")
...
Levins Table of Predictions
   w1 w2 G  W  HG HB EF LF
w1 +  +  0* +  0* +  0* +
w2 -  +  -  +  -  +  -  ?+
G  -  0* +  -  +  -  +  +
W  -  -  -  +  -  +  -  ?+
HG +  0* -  +  +  +  -  -
HB +  +  +  -  +  +  +  ?-
EF +  0* -  +  -  +  +  -
LF +  +  -  ?- -  ?- -  +
> # computaiton of levins analysis algorithm with user defined intervals for
interaction strength
> savannah_lpmin <- levins_predictions(savannah_fires,INT_MIN =
savannah_minv,fname = "savannah_fires_min")
...
> savannah_lpmax <- levins_predictions(savannah_fires,INT_MAX =
savannah_maxv,fname = "savannah_fires_max")
...
```

4. Caspian Sea: a case study

The Ecology of the Caspian Sea: Scenarios for populations decline and possible mechanisms

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4.1. Summary

In the 50s of the last century the Caspian Sea underwent transformations that culminated in the collapse of several fish and mammal species, and the rise in phytoplankton biomass, pushing the system toward eutrophication. Of particular concern was the decline observed in the populations of the Caspian seal (*Pusa caspica*), the sturgeons (*Acipenser spp.*, and *Huso huso*) and the kilka species (*Clupeonella spp*).

In this chapter I aimed at unravelling the mechanisms behind the changes reported for the Caspian Sea ecosystem in the period before the invasion of *Mnemiopsis leidyi*. I mapped the interactive web that characterized the ecological community and analysed it applying the qualitative algorithm of loop analysis, using observed changes in multiple variables as benchmarks for the changes in the variables predicted through the simulations.

From the analysis performed over the model designed for the Caspian Sea it comes that: 1) bony fish and kilkas might play an important role in the system response to pressures; 2) phytoplankton seems to play an important role in the system, in particular negative pressure on this variable produces one of the best rate of predictions and trends match; 3) throughout the analysis, indications from the predictions pointed in the direction that the paths connecting multiple variables of the system and their strength, and from there, the interactions strength between variables, seems to play an important role on the Caspian Sea; 4) from the lack of agreement of the predictions from concurrent inputs and the trends, it can be hypothesised that either the pressures did not all occurred at the same time or their intensity was not the same.

Keywords: Caspian Sea, complex systems, kilkas, press perturbations, population decline, qualitative modelling, Levins loop analysis

4.2. Introduction

In the 50s of the last century the Caspian Sea underwent transformations that culminated in the collapse of several fish and mammal species, and the rise in phytoplankton biomass, pushing the system toward eutrophication (CEP, 2007; Daskalov & Mamedov, 2007; Fazli, Ghanghermeh, & Shahifar, 2017; Aboulghasem Roohi et al., 2010). In 2011, the latest report on the State of the Caspian Sea Environment (UNEP, 2011) highlighted the state of the Caspian Sea as produced by several sources of pressure which include, among others, overfishing, river damming, water pollution and invasion of alien species.

Of particular concern was the decline observed in the populations of the Caspian seal (*Pusa caspica*), the sturgeons (*Acipenser spp.*, and *Huso huso*) and the kilka species (*Clupeonella spp*). The Caspian seal, the only aquatic mammal of this system, counted over 1 million individuals in the early 20th century and diminished to 110,000 individuals in the early 2000s (Dmitrieva et al., 2015; Harkonen et al., 2012; Krylov, 1990). The sturgeons industry, which represented once 80-

90% of the world's caviar production, collapsed to less than 5 thousand tonnes in the 2000s while in the 80s they reached a maximum catch of 27 thousand tonnes (CEP, 2007; UNEP, 2011)(CEP, 2007). The Kilkas caught in the Caspian Sea decayed from 410 thousand tonnes in the 70s to just 54.3 thousand tonnes in 2005 (UNEP, 2011).

The collapse of these species was variously connected with the multiplicity forms of stress that acted on the Caspian Sea (CEP, 2002; H. Dumont, 1995; UNEP, 2011). In the case of kilka species, for example, their decline was associated to the outburst of the invader *Mnemiopsis leidyi* (Bilio & Niermann, 2004; Aboulghasem Roohi et al., 2010) a gelatinous species that played a role in the transformations that characterized the community of the Black Sea ecosystem (Antonio Bodini et al., 2018) and that affected other marine communities. The comb jelly was first detected in the Caspian Sea in 1995 with sporadic presences (signalled by fishermen) and peaked in 2002 (Bagheri, Mansor, Maznah, & Negarestan, 2010; Abolghasem Roohi et al., 2008). A stark reduction of the kilka species catch characterized the Caspian Sea in the years that followed *Mnemiopsis* detection (Daskalov & Mamedov, 2007). The comb jelly should have affected kilka species through competition for the same food (zooplankton) but also through a direct predatory behaviour over the kilkas larvae (Finenko et al., 2006; Shiganova et al., 2001; UNEP, 2011). If kilkas declined strongly in the post-invasion period, it is however known that its decline was already occurring before *Mnemiopsis* appeared in the Caspian Sea. In fact, from its maximum in the 70s (410,000tonnes) it declined by almost 3 times to 132 thousand tonnes in 1996 (UNEP, 2011). Overfishing was indicated as mainly responsible for this negative trend.

Overfishing and hunting affected also sturgeons and Caspian Seal (CEP, 2002; Dmitrieva et al., 2013; Ermolin & Svolkinas, 2018; Harkonen et al., 2012; Kouraev et al., 2004), while an excess input of nutrients perturbed the system from the bottom (UNEP, 2011) . The co-occurrence of multiple stressors makes understanding their role as sources of change in a causal perspective difficult. Although it is commonplace to see a direct causal relation between a driver and the changes shown by its target variable (e.g. kilkas reduction due to overfishing on it), this view represents an oversimplification because i) the impact of drivers percolates from target variables to the rest of the community through pathways of interactions that emerge from the linkage structure of the community; ii) the response of the target variable to its stressor is mediated by the feedback structure created by the linkages. It is well known for example that kilka species represent a bridge that channels the energy flow from primary producers to top predators, in particular sturgeons and seals. Accordingly, overfishing on kilkas may percolate up to its predators inasmuch as perturbing these latter components might have top down effects on their prey. In turn, the response of kilka species to overfishing depends also on the feedbacks that interactions between kilkas and other variables create in the community (Antonio Bodini & Clerici, 2016; Antonio Bodini et al., 2018; P. Lane & Levins, 1977). This scenario suggests that changes in the abundance of the species can hardly be seen as the direct effect of a single driver acting on its target; most likely they are the result of the interplay between the multiple stressors and the structure of the interactions in the community which produces indirect effects. Disentangling this interplay is a prerequisite to understand the causal mechanisms that explain the changes observed in the abundance of the species.

The major aim of this chapter is to contribute to the wider understanding of the mechanisms responsible for changes in the Caspian Sea ecosystem. In particular, we focused on kilkas, a major player of the system for both economic and ecological importance, aiming to elucidate the mechanisms behind its decline in the years before the invasion of the Caspian Sea by the comb jelly *M. leidyi*. I mapped out the interactive web that characterized the ecological community and analysed it by applying the qualitative algorithm of loop analysis (Richard Levins, 1974; Puccia & Levins, 1985). Changes observed in kilkas and in other species, such as Caspian seals, sturgeons and some bony fish species and on nutrients were used as benchmarks for the changes in the level of the variables predicted through the qualitative models assuming different pressures occurring on different target variables. This procedure helps hypothesizing causal mechanisms responsible for the decline of kilkas and the other variables as it unveils the relationship between the sources of change (i.e., the drivers), the structure of the linkages between the variables, and the variation in the level of the variables (J. M. Dambacher & Ramos-Jiliberto, 2007). Specifically the objectives can be defined as: (1) identification of the patterns of variation in response to the different drivers; (2) additional hypotheses, in comparison with mechanisms advanced in the literature, on the role of drivers in respect to the changes that Caspian Sea species underwent in the considered period.

To investigate the effects of the different pressures occurring in the Caspian Sea, the importance of each species in the system response to such pressures and the importance of the level of strength of the interplay between each of the variables, I applied the *loop analysis* qualitative methodology implemented in the *LevinsAnalysis* R package (Pereira et al. in preparation) and generated simulations, both for single and concurrent inputs and by manipulating the interaction strengths of key variable.

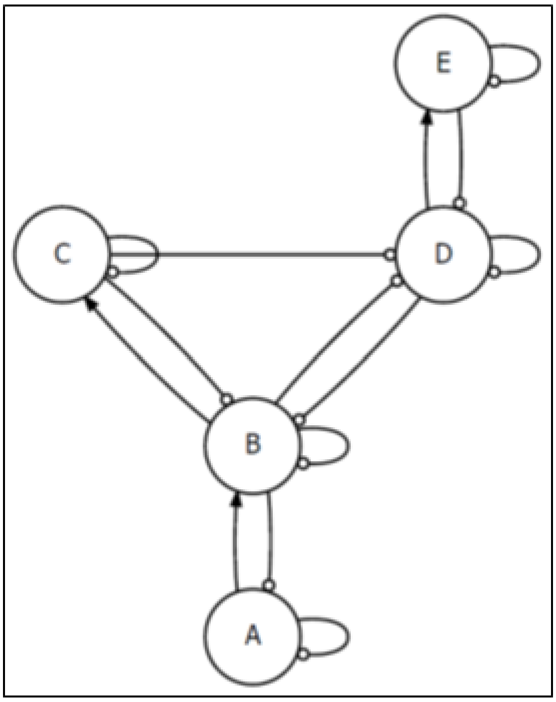
4.3. Materials (and Methods)

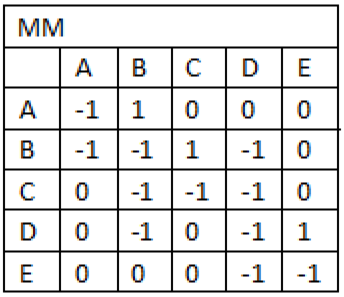
I used qualitative network models of the Caspian Sea ecological community in the form of signed digraphs as pictorial representations of the community matrix. Model outcomes, that are model predictions about the response of the variables to external press perturbations, were compared with trends of species population abundances recorded in the period of investigation. For certain species populations, when data were not available, landings data was used as proxy (Daskalov, Grishin, Rodionov, & Mihneva, 2007). Our models mirror the indications that I found in the literature about the ecological habits of the species so that the structure of the interactions could emerge as a plausible representation of the community under investigation. The models were analysed following the algorithm of loop analysis (Richard Levins, 1974; Puccia & Levins, 1985) which was translated in a *R* package called *LevinsAnalysis* by the authors (Pereira et al., in preparation).

4.3.1. Loop Analysis

Loop Analysis is a qualitative modelling technique that uses signed digraphs to represent networks of interacting variables (Richard Levins, 1974; Puccia & Levins, 1985). Loop analysis allows predicting the direction of change in the level (e.g. biomass, number of individuals) of system variables in response to a parameter alteration or press perturbations on a targeted variable. Press perturbations affect the rate of change of a target variable with effects that propagate to the other species in the community and that are modulated by the feedback structure that is created by the multiple interactions among the variables. Their response can be predicted by the loop analysis algorithm and summarized in a *table of predictions* that becomes a diagnostic tool for the causes of change. Being the algorithm qualitative, the predictions indicate only the direction of change in the equilibrium level of the variables: increase (+), decrease (-) or no change (0).

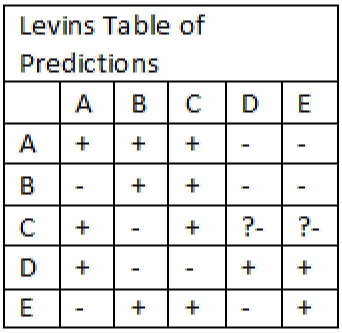
One example is given in Figure 4.1 and summarizes all possible outcomes for the example model depicted in the Figure (model MM). The entries of the table denote variations expected in the level (e.g., biomass) of all column variables in response to positive parameter inputs (i.e., perturbations that increase the rate of change of target variables) affecting any row variable. Conventionally, the calculation considers positive inputs; consequences of negative inputs can be obtained by simply reversing the signs in the table. In models with few variables and/or a limited number of connections, expected changes for the variables can be tracked through the graph anatomy (Antonio Bodini, 1998, 2000). However, when variables and connections increase, multiple pathways of interactions emerge and the probability that pathways have opposite effects increases. In these cases, the model yields ambiguous predictions (i.e., some positive and some negative paths that produce opposite effects). To overcome this problem, I performed our analysis using the tools available in the *R* package *LevinsAnalysis* (Pereira et al. in preparation), which includes a numerical simulation based on a routine that randomly assigns (from a uniform distribution) numerical values in the interval]0,1] to the coefficients of the community matrix (i.e., the coefficients of the links in the signed digraph) .





MM

	A	B	C	D	E
A	-1	1	0	0	0
B	-1	-1	1	-1	0
C	0	-1	-1	-1	0
D	0	-1	0	-1	1
E	0	0	0	-1	-1



Levins Table of Predictions

	A	B	C	D	E
A	+	+	+	-	-
B	-	+	+	-	-
C	+	-	+	?-	?-
D	+	-	-	+	+
E	-	+	+	-	+

Figure 4.1: Model *MM* signed digraph and corresponding adjacency matrix and table of predictions from LevinsAnalysis R package (Pereira et al. in preparation). In the graph (on the left), positive interactions are denoted with arrow-headed links while negative interactions are visualized with circle-headed links. Values on *MM* adjacency matrix (on the top right) correspond to the qualitative effect of variable *i* (row) in variable *j* (column). Signs in the table of prediction (on the lower right) correspond to the expected direction of change in the level of the column variable *j* due to the pressure in the row variable i.

4.3.2.Data structure and trends

The reliability of our model in describing the Caspian Sea community was tested against abundance trends of some of the variables included in the model. Such trends were deduced from the literature through a meta-analysis in which a number of papers were scrutinized to reconstruct qualitatively the trends. This strategy was necessary to overcome the lack of the original abundance data that would have been used to compile a data set to be exploited for the purposes of this investigation. Also, this procedure highlighted lack of coherence about the trends of certain species as they were reported in different pieces of the literature. The procedure I adopted allowed me identifying the direction of the trends for the populations but seriously impaired our capability to perform statistical analysis about the variations in the trends and that could support effectively model predictions (Antonio Bodini & Clerici, 2016; Antonio Bodini et al., 2018).

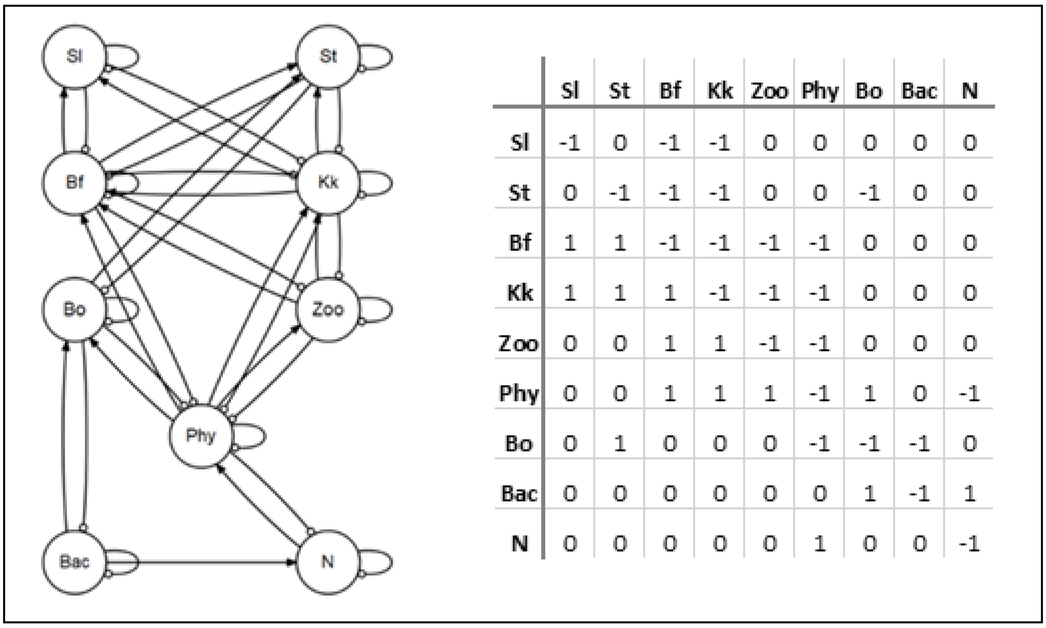
Despite the difficulties to obtain data about the trends for all the species, still, general indications about the direction of the trends for multiple species of our model could be obtained. I summarize these trends in Table 4.1. Information regarding the literature from which these trends were drawn can be seen in ***Annex A – Species trends***.

Seals	Sturgeons	Bony Fish	Kilkas	Zooplankton	Phytoplankton	Benthic Organisms	Bacteria	Nutrients
-	-	-	-					+

Table 4.1: Direction of trends of the variables of our model of the Caspian Sea in the pre-invasion period (pre-1998). The "+" indicates a positive trend, i.e., an increase in the biomass level of the species; the "-" symbolizes a negative trend, i.e., a decrease in the biomass level of the species.

4.3.3.Model construction, validation and analysis

The model for the Caspian Sea ecological community was constructed based on the trophic and non-trophic interactions among the major groups as they are described in the literature. The model discussed here considers the community structure before the outburst of the comb jelly *M. leidyi* that occurred in 1998. That is, it describes the community structure for the period 1950 - 1998. From literature a complex model, with 23 variables and 223 links between nodes, was generated. Increased complexity in a system increases not just the difficulty in analysis to discern any possible information, but also leads to generation of tables of predictions with a higher percentage of indeterminacies (predictions where the value assigned is either *0**, *?+* or *?-*). For the sake of simplicity, I collapsed our network into a model with 9 variables and 38 links between nodes. The model and its community matrix are represented in Figure 4.2. In this model, I maintained the major species and functional groups that are known to play an important role on the Caspian Sea, that is, species that have been recognized as of ecological or economic importance. Next decision had to be taken as to which interactions should be considered for the skeleton of the model. I included only those interactions that could be deduced directly from the literature about the Caspian Sea and, in general, from the literature describing the ecology of the species in general (Froese & Pauly, 2019; Kosarev & Yablonskaya, 1994). In the process of model reconstruction from ecological facts or evidences often uncertainties emerge about the type of interactions between the variables. When in doubt about the existence or the importance of a given interaction building alternative models is the best strategy (Antonio Bodini et al., 2018). In this analysis, I did not consider alternative graphs; rather I took advantage of the facilities that the *LevinsAnalysis* R package (Pereira et al. in preparation) provides to simulate interaction strengths to investigate the role of specific interactions.



	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
Sl	-1	0	-1	-1	0	0	0	0	0
St	0	-1	-1	-1	0	0	-1	0	0
Bf	1	1	-1	-1	-1	-1	0	0	0
Kk	1	1	1	-1	-1	-1	0	0	0
Zoo	0	0	1	1	-1	-1	0	0	0
Phy	0	0	1	1	1	-1	1	0	-1
Bo	0	1	0	0	0	-1	-1	-1	0
Bac	0	0	0	0	0	0	1	-1	1
N	0	0	0	0	0	1	0	0	-1

Figure 4.2: Signed digraph describing the community structure for the pre-invasion period of the Caspian Sea by M. leidyi (a) and its adjacency matrix (b). All interactions refer to trophic relationships or consumption of resources (i.e., see the connection from nutrients to phytoplankton. Keys for nodes: seals (Sl), sturgeons (St), bony fish (Bf), kilkas (Kk), zooplankton (Zoo), phytoplankton (Phy), benthic organisms (Bo), bacteria (Bac), nutrients (N).

Trends were searched in the literature for the species of interest to serve as benchmarks to verify model predictions and define model reliability. A reliable model is one that correctly predicts the observed changes. Although in ecology, often the entry point of a parameter change (a perturbation) is unknown, in the case of the Caspian Sea, however, several literature sources agree in identifying particular types of perturbations that affected the system during a given period which I summarized in Table 4.2.

Seals	Sturgeons	Bony Fish	Kilkas	Zooplankton	Phytoplankton	Benthic Organisms	Bacteria	Nutrients
-	-	-	-					+

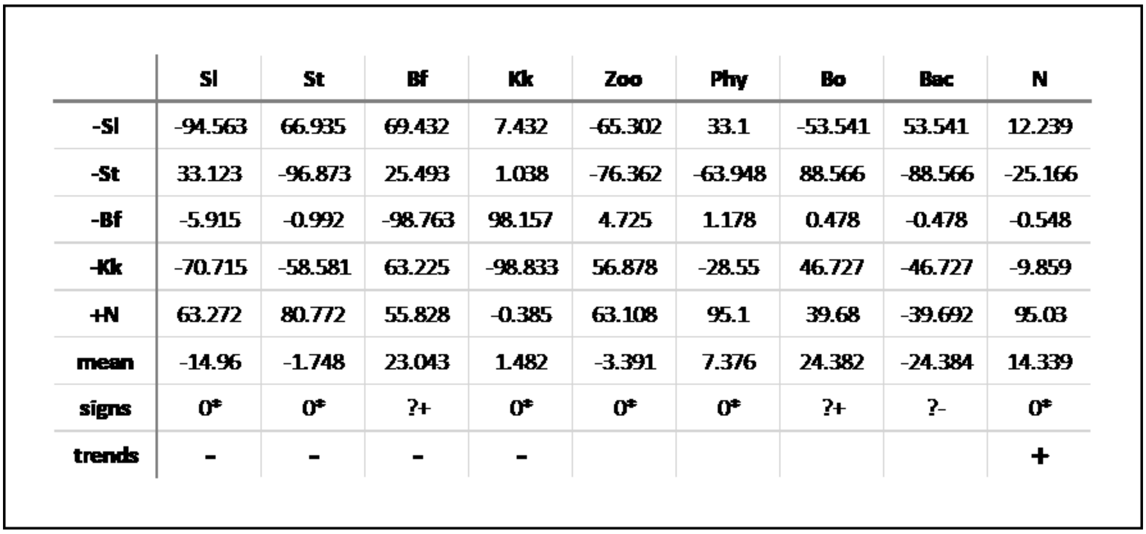
Table 4.2: Input signs of pressures in the Caspian Sea species. A negative sign ("-") signifies a pressure that causes a reduced rate of change for that variable; a positive sign ("+") signifies a pressure that causes an increase in the rate of change for the variable, in accordance with the meaning of the input (see Methods).

Using the *LevinsAnalysis* package (Pereira et al. in preparation) I performed simulations for the effect of single and concurrent inputs in the system taking in account the press perturbations listed in Table 4.2. According to the qualitative nature of the algorithm, the outcomes of a table of predictions describe the expected direction of change in the equilibrium level of the column variables (i.e., biomass, number of individuals) due to a positive parameter input on the row variables (the predictions for a negative input can be obtained by sign inversion). For concurrent inputs, the expected direction of change in the equilibrium level of a variable is listed as the sum of the effects caused by each input on the entry point variables considered. The predictions were obtained through simulations based on quantification of the interaction coefficients (i.e., link strength). Values of link strength were assigned randomly in the uniform distribution within the interval]0,1], with exception for the tests on the importance of strength of interaction, where strength of interaction was changed by us to reflect specific scenarios (in ***Annex B – R code for simulations*** is given the code to perform the analysis). The predictions for the direction of change obtained by the simulations on our model were compared with the biomass trends for the period of 1950-1998 (Table 4.1).

4.4. Results

4.4.1. Model validation

After assessing model stability, I computed the table of predictions simulating concurrent pressures as they occurred in the Caspian Sea. Such press perturbations are summarized in Table 4.2 as signs indicating variations in the rate of change of the variables, increase (+) or decrease (-) as they likely were produced by the types of perturbations affecting the single components. Table 4.3 summarizes the predictions obtained from simulating the press perturbations listed in Table 4.2. Variations in the abundance trends of some of the components are listed in the last row of Table 4.3, according to the data set at disposal. The penultimate row of Table 4.3 indicates the possible net effects of the multiple inputs, that is the concurrent predictions.



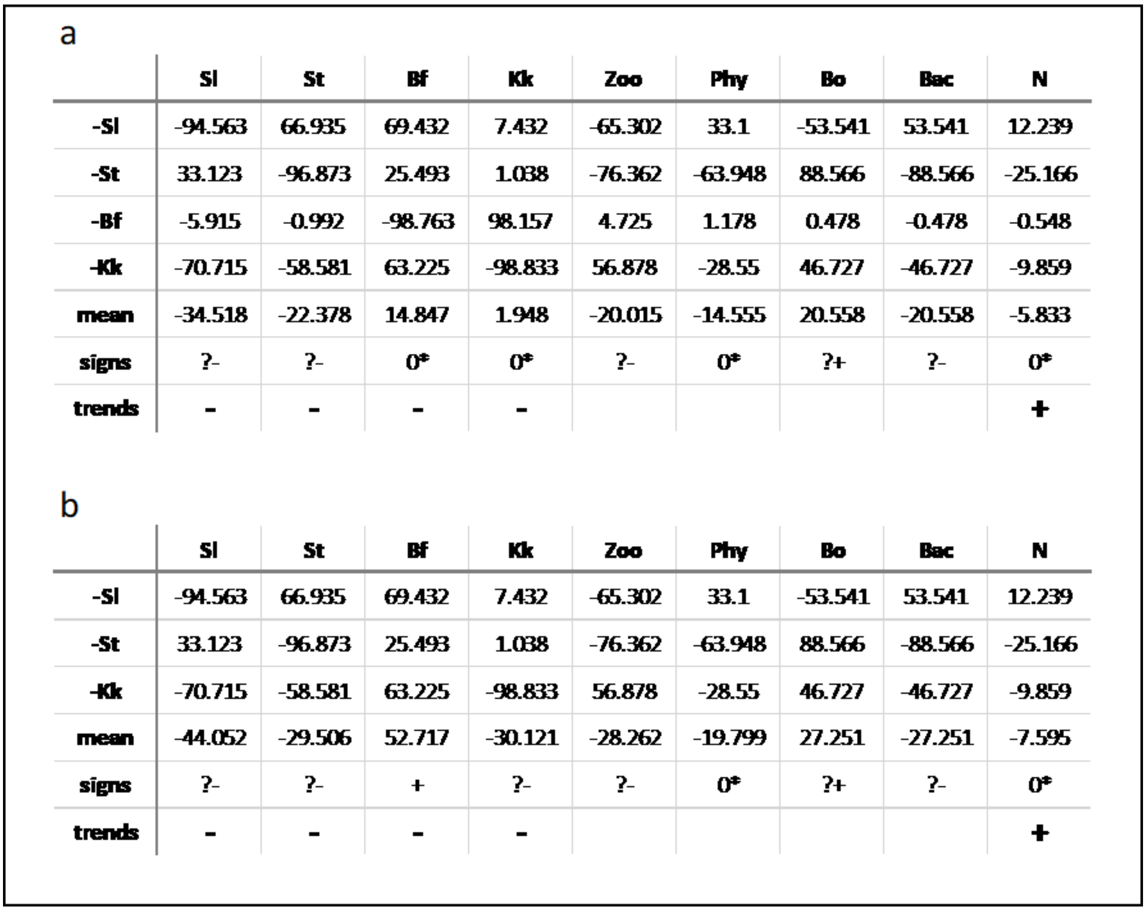
	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-94.563	66.935	69.432	7.432	-65.302	33.1	-53.541	53.541	12.239
-St	33.123	-96.873	25.493	1.038	-76.362	-63.948	88.566	-88.566	-25.166
-Bf	-5.915	-0.992	-98.763	98.157	4.725	1.178	0.478	-0.478	-0.548
-Kk	-70.715	-58.581	63.225	-98.833	56.878	-28.55	46.727	-46.727	-9.859
+N	63.272	80.772	55.828	-0.385	63.108	95.1	39.68	-39.692	95.03
mean	-14.96	-1.748	23.043	1.482	-3.391	7.376	24.382	-24.384	14.339
signs	0*	0*	?+	0*	0*	0*	?+	?-	0*
trends	-	-	-	-					+

Table 4.3: Table of concurrent predictions for pressures on the Caspian Sea model and comparison with the observed trends for each of the species. Row values indicate the percentage of either positive or negative matrices that determined the sign of each affected value (column) due to the input pressures (row variables). Row "mean" and "signs" indicate the cumulative impact generated by the concurrent effect of the multiple inputs, while the "trends" row indicates the trends obtained from literature for each node. Keys for the nodes: seals (Sl), sturgeons (St), bony fish (Bf), kilkas (Kk), zooplankton (Zoo), phytoplankton (Phy), benthic organisms (Bo), bacteria (Bac), nutrients (N).

From the results of the model validation test summarized in Table 4.3 0 matches between predictions and the trend variations were obtained. This means that the model is not able to reproduce the observed patterns of abundance. However the graph is structurally coherent with the structure of the interactions as it was conceived by Kosarev and Yablonskaya (1994, Froese and Pauly, 2019). Nevertheless, although the model seems to be sound according to other authors who too depicted the structure of the interactions in the Caspian Sea, it does not work fine in predicting the observed changes in the level of the variables. Many reasons can justify these outcomes. Several problems arose with the data. Abundance trends used for the model reliability test were from different pieces of the literature and so they reflected different experimental conditions, different areas of sampling and combined data from various regions that were presented in different studies. The heterogeneity of the data makes difficult to compare results in a meaningful way. Here, I followed the whole basin approach and combined data from different regions to obtain average values for the biomass of the main pelagic components. Also, there is the problem of the timing of the inputs. Precise indications about when specific inputs occurred in the system do not exist and also, the time of response of the system to press perturbation is a critical point. So, despite these inconveniencies I can consider the graph a coherent description of the structure of the interactions although an in-depth revision of the data would be needed to compile a more coherent database to be used as benchmark for model predictions. A critical point in this respect is that most of the documents presenting data are written in Russian or other languages that are not in use in the scientific community. Also, with a total of 1463 possible simple paths (i.e. paths that never repeat any of the nodes twice), some confounding mechanism may be in action. By analysing the results of the concurrent predictions we can see that the mismatch between trends and predictions is mostly due to the *0** prediction (in 4 out of 5 comparisons the model prediction is of this type), which means a balance between the effect of negative and positive paths affecting the target variable.

This outcome points out one aspect about the complexity of the system. A *0** prediction summarizes the balance between multiple paths carrying opposite effects. Nonetheless this balance is the result of a statistical rule that assign a quasi-compensation when the difference between the percentage of positive predictions and percentage of negative predictions of the simulated matrices is in the range from [-20, 20] (see ***Chapter 2: 2.1.2 Interaction Strength***). This implies that if this range is restricted (new rules of selection) likely a tendency to change will emerge. In that case, in fact, even small differences in the balance between positive and negative signs can be detected and produce a prediction sign different from the *0**. Possibly some of the pressures might have played a stronger role than others and may not have occurred concurrently. I assumed the input occurred concurrently because from the literature it was not possible to assess the timing of their occurrence.

In particular, I considered two alternative cases with different schemes of concurring pressures: 1) overexploitation of seals and the fish only (no nutrient load to the system); 2) overexploitation of seals, sturgeons and kilkas. The results I obtained from the comparison between predictions and the observed trends improved over that from when all pressures were considered concurrent. Table 4.4 summarizes the results of the alternative scenarios, with the models showing 2 and 3 matches out of 5 trends, respectively. A third scenario, in which I considered nutrient concentration trend to be 0 (from literature there are indices that in last few years of our period of analysis, some improvements in wastewater treatment plants may have reduced the level on nutrient input in the system), and considering only the negative inputs in seals, sturgeons and kilkas I obtained a match of 4 out of 5 trends (results in ***Annex C – Complimentary analysis: Model validation***).



a

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-94.563	66.935	69.432	7.432	-65.302	33.1	-53.541	53.541	12.239
-St	33.123	-96.873	25.493	1.038	-76.362	-63.948	88.566	-88.566	-25.166
-Bf	-5.915	-0.992	-98.763	98.157	4.725	1.178	0.478	-0.478	-0.548
-Kk	-70.715	-58.581	63.225	-98.833	56.878	-28.55	46.727	-46.727	-9.859
mean	-34.518	-22.378	14.847	1.948	-20.015	-14.555	20.558	-20.558	-5.833
signs	?-	?-	0*	0*	?-	0*	?+	?-	0*
trends	-	-	-	-					+

b

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-94.563	66.935	69.432	7.432	-65.302	33.1	-53.541	53.541	12.239
-St	33.123	-96.873	25.493	1.038	-76.362	-63.948	88.566	-88.566	-25.166
-Kk	-70.715	-58.581	63.225	-98.833	56.878	-28.55	46.727	-46.727	-9.859
mean	-44.052	-29.506	52.717	-30.121	-28.262	-19.799	27.251	-27.251	-7.595
signs	?-	?-	+	?-	?-	0*	?+	?-	0*
trends	-	-	-	-					+

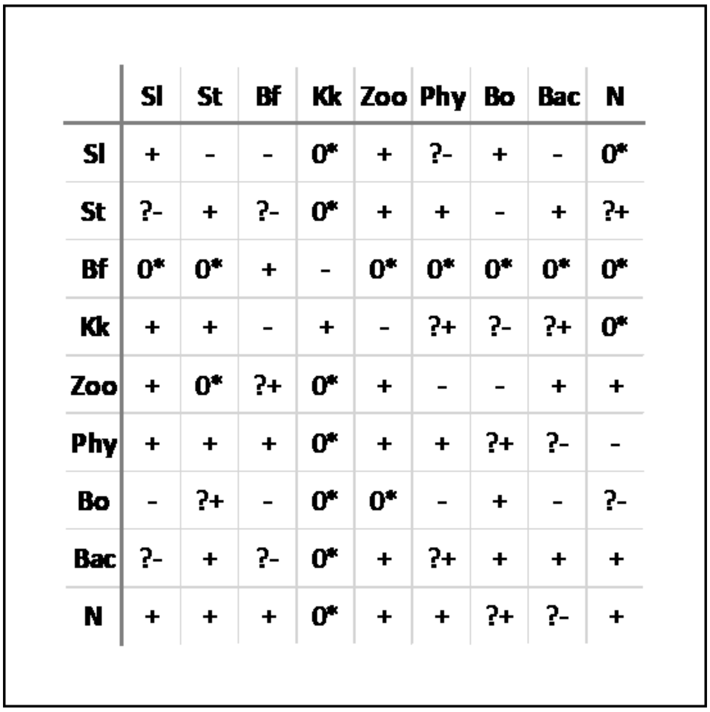
Table 4.4: Table of concurrent predictions for alternative schemes of pressures on the Caspian Sea model and comparison with the trends for each of the species. Row values indicate the percentage of either positive or negative matrices that determined the sign of each affected value (column) due to the input pressures (row variables). Row "mean" and "signs" indicate the cumulative impact generated by the concurrent effect of the multiple inputs, while the "trends" row indicate the trends obtained from literature for each node. Keys for the nodes: seals (Sl), sturgeons (St), bony fish (Bf), kilkas (Kk), zooplankton (Zoo), phytoplankton (Phy), benthic organisms (Bo), bacteria (Bac), nutrients (N).

4.4.2. Table of Predictions

According to the literature the main drivers that affected the Caspian Sea between the 1950's and the 1990's were i) overexploitation of faunal resources, ii) damming of the main rivers that feed the basin (most important of all the Volga river), and iii) the increase in nutrient loading. Although most of the effect of some of these pressures showed up after the 50's, some of these were already present. The damming of rivers that fed the Caspian Sea started in the 30's. A particular case is the damming of the Volga river which began in the 30's to be completed in 1961 (CEP, 2002; Kosarev & Yablonskaya, 1994; RusHydro, 2019) This project prevented species to access the upriver spawning grounds. In particular the Caspian sturgeon's spawning grounds greatly shrank (e.g. the beluga sturgeon saw 90% of its spawning grounds lost (CEP, 2002; UNEP, 2006)).

Fishing in the Caspian saw not just an increase in the number of fishing vessels, but also in the modernization of its fleets in the middle of the century, which lead to an increase in the fishing capacities of the multiple fishing industries such as that of kilkas (Kosarev & Yablonskaya, 1994), and with the introduction of some techniques, also led to the increase in by-catch of other species such has seals and sturgeons (Dmitrieva et al., 2013; Ruban & Khodorevskaya, 2011). Also, illegal catch is a very serious threat , and for some species, it far surpasses the legal catch (Raymakers, 2002; UNEP-WCMC, 2010). Pollution has affected the Caspian Sea in two forms: toxin loading and nutrient enrichment. The former might have affected all the trophic levels of the ecological community and the latter entered as a perturbation at the very bottom of the food web. The level of toxins in the Caspian saw a steady and rapid rise with the development of the oil from the middle of the century onwards, together with the input from different industrial developments all along the littoral of the sea (CEP, 2002, 2007; UNEP, 2011). Nutrient enrichment too has been a constant in the sea, both from natural causes, such as the inundation of shallow lands upon the rise of the sea level in the 70’s (Kosarev & Yablonskaya, 1994), and due to run-offs from agriculture and domestic waters. The population in the littoral of the Caspian have steadily and rapidly grown, in particular in the last decades of the past century, albeit without proper development of waste-water treatment plants (CEP, 2002, 2007; UNEP, 2011).

Table 4.5 shows the result of the simulations of the loop analysis algorithm over the Caspian Sea model from Figure 4.1, that is, in the table are presented the predictions for the model.



	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
Sl	+	-	-	0*	+	?-	+	-	0*
St	?-	+	?-	0*	+	+	-	+	?+
Bf	0*	0*	+	-	0*	0*	0*	0*	0*
Kk	+	+	-	+	-	?+	?-	?+	0*
Zoo	+	0*	?+	0*	+	-	-	+	+
Phy	+	+	+	0*	+	+	?+	?-	-
Bo	-	?+	-	0*	0*	-	+	-	?-
Bac	?-	+	?-	0*	+	?+	+	+	+
N	+	+	+	0*	+	+	?+	?-	+

Table 4.5: Table of predictions for pressures on the Caspian Sea model. Signs in the Levins table of prediction are the expected direction of change in the level of the column variables for a pressure on the row variable. Keys for the nodes: seals (Sl), sturgeons (St), bony fish (Bf), kilkas (Kk), zooplankton (Zoo), phytoplankton (Phy), benthic organisms (Bo), bacteria (Bac), nutrients (N).

Seals

In the past century the Caspian seals declined considerably, due to multiple causes such as hunting and by-catch. The scenario that may describe the conditions for this species is one that includes a negative input on seals and kilkas (*-Sl* and *-Kk* in Table 4.5). It is possible to observe that for both cases a negative prediction would be obtained, matching the observed trends for Seals. Another food source for Seals, although not as important as the kilkas, is bony fish, which was heavily exploited. When considering a negative input on bony fish (*-Bf*) the predicted result for the effect on seals did not match with the trend. Nutrient is a particular case, since it affects negatively every species in the system due to toxin loading, represented in the loop analysis as a negative input directly on seals, (*-Sl* in Table 4.5), but also has the potential to affect it positively with nutrient enrichment on the lower levels of the trophic system, which kilkas and bony fish feed upon. A positive input on nutrients (*+N* in Table 4.5) goes in the opposite direction than expected from the trend so matching is possible if a negative input is taken into account. Taking the analysis a step further I verified the effect of the multiple scenarios of concurrent pressures on seals and all agree with the trend of decline for this species, with the best results associated with negative pressure on both seals and kilkas (results in ***Annex C – Complimentary analysis: Concurrent predictions - Seals***).

Sturgeons

The spawning grounds for sturgeons shrank dramatically with the damming of multiple rivers. Also, the fishing pressure constantly increased throughout the century, along with by-catch and toxic loading. The predicted effect of these pressures, all generating a negative input on St (*-St*) matches with the observed trends, which indicates a decline of the sturgeons' populations. Reduction in kilkas and bony fish from overfishing, both preys of sturgeons, overall lead to predicted decline of sturgeons (decrease for a negative input on kilkas and no change associated to a negative input to bony fish. When considering a positive input on nutrients (*+N*) opposite predictions in relation to the trends were obtained. Concurrent predictions were calculated to include multiple scenarios of these pressures, and with the exception of the scenario with nutrient enrichment on top of overfishing for sturgeons, bony fish and kilkas (which produced inconclusive results), all concurrent prediction scenarios agree with the trends of decline in sturgeons population. Overfishing of sturgeons and kilkas revealed to be the scenario with the strongest result (results in ***Annex C – Complimentary analysis: Concurrent predictions - Sturgeons***).

Bony fish

River damming reduced bony fish's spawning grounds. Also, perturbations were due to overfishing and toxins loading. The predictions (Table 4.5) for a negative input to bony fish (*-Bf*) match with the trends. A negative input on kilkas (*-Kk*), produces a prediction with opposite sign of that of the observed trend for its predator. A positive input to Nutrients (*+N*) is predicted to produce changes that are not in agreement with the observed trend for this component. Although no trends about both zooplankton and phytoplankton were at disposal in the literature it is possible to see that a positive input on each of these two groups (*+Zoo*/ *+Phy*) would predict a change in bony fish opposite to the observed trend for this species; a negative input occurring in any of them would predict a change in agreement with the observed trend. Predictions about the level of bony fish match with the observed trend for this species for most of the concurrent pressure scenarios with input on zooplankton and phytoplankton developed (see in ***Annex C – Complimentary analysis: Concurrent predictions - Bony fish***). To consider also is the effect on bony fish species from the depletion on the population levels of its predators, seals and sturgeons, concurrently with its own pressures (see in ***Annex C – Complimentary analysis: Concurrent predictions - Bony fish***). From the concurrent predictions results for these hypotheses it comes that the only case with a match between predictions and the observed trends for the effect of negative inputs in the system on bony fish is when we consider only the concurrent negative in bony fish and sturgeons.

Kilkas

With the increase of efficiency and effort, fishing pressure on the kilka species augmented considerably. Model predictions confirm the decline of this component if subjected to a negative input (*-Kk* in Table 4.5). Thus, in this case predictions match with the observation. From the 1950s to the 1970s years of maximum fishing effort on these populations its predators, seals, sturgeons and bony fish all suffered from negative pressures as well. By observing the signs in Table 4.5 it comes that a null change in the level of kilkas follows a negative input on top predators (*-Sl* and *-St*). A negative input on its other predator (*-Bf*), is expected to increase kilkas. A positive input on nutrients alone would cause no change in kilkas level. Although no abundance trends could be reconstructed for zooplankton and phytoplankton, akin to the bony fish case it would be interesting to see the effect that an hypothetical input on these two nodes would cause on kilkas, but no change is expected in the levels of kilkas. Interestingly enough, no change in the expected level of kilkas emerged from the simulation despite the observed trend indicating a decline in the population. Some concurrent input scenarios where drawn and tested for the possible concurrent inputs with kilkas overfishing (see ***Annex C – Complimentary analysis: Concurrent predictions - Kilkas***). The only cases in which an expected negative change is predicted is the concurrent effects of over-exploration of both kilkas and its top predators (seals and sturgeons); the other scenarios combinations again give a no change expected prediction. The concurrent effect with nutrient enrichment is also predicted to lead to kilkas decrease; but when this pressure is coupled with input on its predators no change is expected. The hypothetical case of an input into zooplankton and phytoplankton, regardless if an input in one or concurrently on both (independently of the sign of the input), the expected result is always the same, an expected negative change in kilkas population levels in accordance with the observed trends. In the case of kilkas there seems to be no one concurrent prediction scenario that is much better than the other, with only the single extra concurrent input added being the cases that presented a slightly higher strength (all results in ***Annex C – Complimentary analysis: Concurrent predictions - Kilkas***).

Nutrients and toxic compounds

Nutrient loading increased noticeably with economic development and the associated increase of the human population living along the Caspian coast. Nitrogen and Phosphorous but also, toxic substances such as hydrocarbons and DDT were released in the Caspian Sea. The effects of toxicity, which was documented to increase the mortality of seals and of the fish compartments, as already been discussed above for each species, concomitantly with other negative inputs affecting each species, since through this analysis the effect of different pressures of a same sign cannot be discerned from one another. When we consider the concurrent effect on the system from positive input on Nutrients and negative input on seals and the fish comportments (all together; Table 4.3), it comes out that the predictions do not match the observed trends for any of these species. When we consider the concurrent effect that nutrient enrichment and negative pressure on seals, sturgeons, bony fish and kilkas (individually) we obtained that for the Caspian Sea top predators these predictions fail to match with the trends and only for the scenarios with bony fish and kilkas we see a match between trends and the predicted effect for these species. (results in ***Annex C – Complimentary analysis: Concurrent predictions - Nutrients***).

4.4.3. Interaction Strength

The *LevinsAnalysis* R package (Pereira et al. in preparation) offers the user the opportunity to include and varying link magnitude in the analysis. Intensity values can be selected randomly from uniform, normal or pareto distributions. Also, it is possible to define the magnitude of specific links in the case its intensity is known from experimental investigations or from the literature. In the analysis presented so far, I extracted link magnitude from the uniform distribution. But it is known that any interaction between species may have a defined range of intensities. For example, even though seals predate both on kilkas and bony fish, its main food source is kilkas; therefore, the intensity of this interaction can be set up to be stronger than that of the interaction between seals and bony fish.

This manipulation of the interaction strength makes the model ecologically more reliable in the sense that it mimics better the ecological reality. It also allows investigating the sensitivity of the response of the variables to external inputs. The effect of changing the strength of the links that constitute the network of the Caspian Sea is represented by the barplot depicted in Figure 4.3. It highlights the percentage of prediction signs changes. Predictions are mostly sensitive to the magnitude of the negative effect of sturgeons on bony fish [*St -o Bf*] and the positive effect of zooplankton on bony fish [*Zoo -> Bf*], with the former showing a higher confidence interval. Overall the higher sensitivity does not exceed the 15% of the predictions. The link whose variations in magnitude affects less the predictions is the positive effect from bacteria to nutrients [*Bac -> N*], with a percentage of changing predictions that is below 5%.

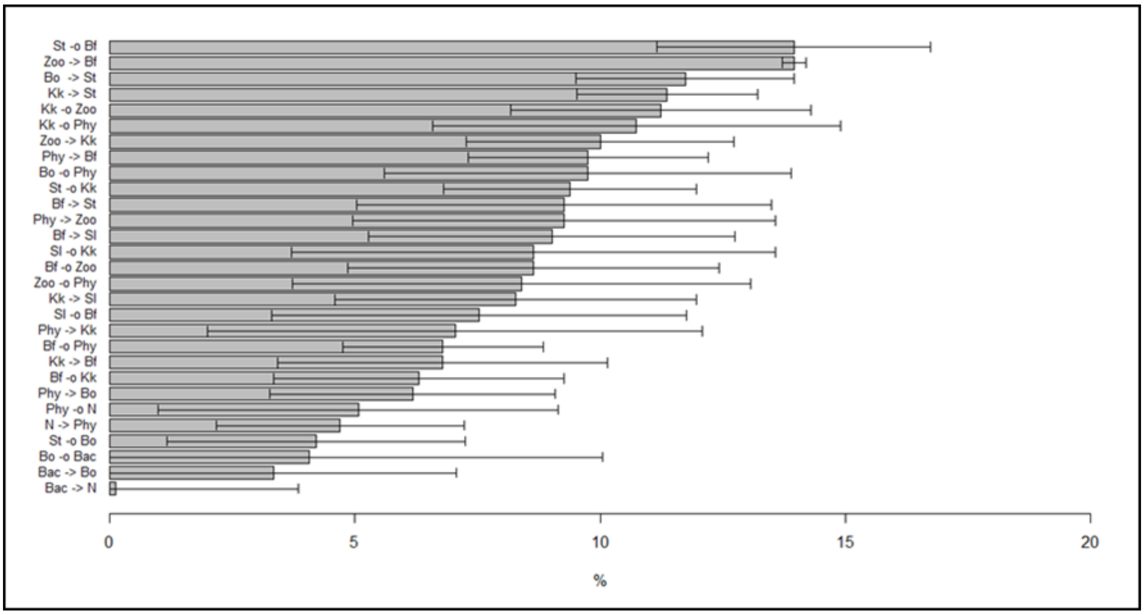


Figure 4.3: Number of deviations in the signs of the table of predictions of the Caspian Sea model due to changes in the strength of interactions (whiskers signal the interval of confidence). The different interaction links are along the Y axis, and the percentage of change in the predictions are reported along the X axis. Keys for the nodes: seals (Sl), sturgeons (St), bony fish (Bf), kilkas (Kk), zooplankton (Zoo), phytoplankton (Phy), benthic organisms (Bo), bacteria (Bac), nutrients (N).

From Figure 4.3 it is also possible to see that nodes that appear more frequently on the top 10 links are kilkas and sturgeons. Apart from the positive link from zooplankton to benthic organisms, which has the smallest interval of confidence, most of the links present fairly large intervals of confidence, with the two links with the highest interval of confidence being the positive link from phytoplankton to kilkas [*Phy -> Kk*] and the negative link from benthic organisms to bacteria [*Bo -o Bac*], with the latest having its interval of confidence left side at 0 and its right side at above the 10% mark. The results from this table serve to indicate which links would produce a higher change in the table of matrix predictions if I changed their strength values.

A further scenario was designed where table of predictions were computed with strength matrices values fixed at defined levels for the top 5 interactions presented in Table 4.3. Strength variations were performed on single links or various combinations of these top 5 interactions. Although none of the resulting simulations predicted better results than those obtained previously for the model validation analysis, there was an improvement in the resolution of some of the predictions, with some ambiguities being solved, in particular the *0** predictions made along the bony fish row and kilkas (results in ***Annex C – Complimentary analysis: Strength interaction***).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
Sl	+	-	?-	?-	+	?-	?+	?-	0*
St	?-	+	-	?+	+	+	-	+	0*
Bf	0*	?+	+	-	?+	0*	-	+	?+
Kk	+	0*	-	+	-	?+	0*	0*	?-
Zoo	+	0*	+	?-	+	-	-	+	+
Phy	+	+	?+	0*	+	+	?+	?-	-
Bo	-	+	-	0*	0*	-	+	-	?-
Bac	?-	+	?-	?+	?+	?+	+	+	+
N	+	+	?+	0*	+	+	?+	?-	+

Figure 4.3: Table of predictions for pressures on the Caspian Sea model, with changes in the values of interactions for the top 5 links of Figure 4.3. Keys for the nodes: seals (Sl), sturgeons (St), bony fish (Bf), kilkas (Kk), zooplankton (Zoo), phytoplankton (Phy), benthic organisms (Bo), bacteria (Bac), nutrients (N).

4.5. Discussion and Conclusion

Model construction is not a trivial process. From the choice of variables to interactions one should put much effort in the attempt to select components that play an ecological role and identify links that at best describe the way variables interact. The analytical approach that I used to test the models validity, by computing the effect of the multiple pressures on the system that occurred within the study period (1950-1998) and matching those predictions with the general trends (Table 4.1) of the models variables during the same period dictated that our model was unfit (Table 4.3). As discussed above, the information taken from the literature indicates that the model presented here is reliable descriptions of the Caspian Sea network. When the effect of different pressures are considered independently from one another the percentage of matches between predictions and the trends increases (Table 4.4). Therefore the incongruence arisen in the exercise of testing model reliability, coupled with the structural soundness of the proposed structure of the interactions that emerged from the literature and the various scenarios of concurrent inputs suggest that : 1) not all of the pressures occurred concurrently and their relative intensity might have affected the overall outcomes in a way that could not be grasped by the simulations; 2) model validation is a complex process, which requires great assimilation of facts, ecological understanding and coherent indication from the literature as well as well-structured and complete data sets.

Table 4.5 highlights that the entry point of external perturbations for which a higher number of predictions match with abundance trends is kilkas. In particular, for a negative input on this variable (*-Kk*), predictions for 3 out of 5 variables match with real trends for seals, sturgeons and kilkas itself. This result points to the importance of Kilkas and its overfishing as an important factor for the dynamics of the entire system. Input on bony fish leads to many *0** predictions. They are indicative of a compensation of effects between paths of opposite sign. This result can be interpreted as a sign of the bony fish node centrality and high level of connectance involving this variable. But this is not the only variable for which this conclusion holds. A table of predictions reads from the row variables (target of perturbations) to the column variables (effect variables), i.e. the outbound effect, and therefore information is taken row by row. But information can also be retrieved down the columns which gives the effect column species suffers from inputs entering through the row variable (inbound effect). Reading the table by columns kilkas node once again stands out. It appears rather insensitive to external perturbations entering through any variable, as in only two cases its abundance is expected to vary (input on bony fish and on kilkas) whereas in all the other cases (*0**) is the outcome. This suggests that kilkas is structurally central in the system. Looking at predictions due to concurrent inputs (see ***Annex C – Complimentary analysis: Concurrent Predictions***) the two scenarios for which a higher level of matches with the trends emerges (4 matches) both include negative pressure on bony fish and kilkas (scenarios: *-Bf and -Phy; -Kk and -Phy; -Kk, +Zoo and -Phy*). Considering phytoplankton as entry point of perturbations reducing its rate of change (negative input) expected changes for 4 variables are coherent with observed trends. Overall, bony fish and kilkas play different roles in the spreading of effects due to external perturbations. Input entering through bony fish spread only to kilkas and bony fish itself whereas the other variables experience null changes or of very low magnitude due to the compensation of effects associated to paths of different sign. On the other hand input entering to kilkas is likely to spread all over the system (only nutrients do not change their level) but at the same time it is the most resistant species in the system as its level is predicted to change only for input on itself and on bony fish. For these reasons kilkas seem to play an important role from the structural point of view.

Another outcome that is worth mentioning is that bony fish and kilkas appear as true competitors. They feed on the same resources (zooplankton and phytoplankton) but there is also a direct interaction between them as bony fish preys upon kilkas. This asymmetric competition (sensu Levins, 1979) nevertheless, does not mitigate the reciprocal inhibition which appears clearly when input on kilkas and on bony fish occurs, in both cases the two variables change in the opposite directions, revealing the same patterns of correlation than two competitors would show (Giavelli, Bodini, & Rossi, 1990). In the light of these results it can be said that overfishing on kilkas might have had consequences well beyond the variable itself. Consequences of input to phytoplankton confirm the observed trends in 4 cases. However, despite this result the input to these variables may remain fictitious as there are no indications in the literature that some driver acted on phytoplankton and further review of the literature about possible pressures on phytoplankton and their temporal occurrence will clarify this point. However, the damming of the Volga river, and the subsequent years of constant change in the Caspian Sea level, might be put forward as an hypothesis for the possible negative input into phytoplankton.

As discussed above, interaction strength highly affects predictions. In theory, the compensation between paths of different sign which produce a *0** prediction could be solved by playing with link intensity so that pathways may differentiate their effects. The analysis of interaction strength variations shows that substantial modifications in the structure of the predictions does not follow from changes in link magnitude (max 20% of changes in predictions follows variations of link strength), but some of the links have the greatest share of the overall variation. Interactions whose variation mostly change patterns of model predictions are shared by bony fish and kilkas (see Figure 4.3). From the concurrent input scenarios where we changed the interaction strength of the top interaction pairs, it comes that the only cases where we obtain a change away from null effect (*0**), both on bony fish row (effect that input on itself has on others) and on kilkas column (effect that input on other have on itself), is when we consider all these interaction strength changes together (Table 4.6). All these results seem to point on the direction of the importance of bony fish and kilkas nodes within the network and its response to pressures, but offering divergent views on the cause of this importance, from one side their inbound importance, from the other their outbound importance (both bony fish and kilkas have their importance, in both results, pointing in different directions). To solve this problem, and the two seemingly results can be brought together to explain the importance of these two nodes and what role they play and in which way they play it in the systems response to pressures, further analysis into the specific paths involving each of these variables and their specific lengths, nodes involved and strengths, should be done. An hypothesis that can be made is that although these species may play an important role in the system, the intensity of their interactions with others might not be so important, but rather the interactions of other variables, through which the paths connecting bony fish and kilkas to the rest of the system rely on.

From Table 4.5 and subsequent concurrent input analysis (see ***Annex C – Complimentary analysis: Concurrent input***) a positive input on nutrients leads to low levels of matches between trends and predictions. This input is due to nutrient enrichment, which seems to not be able to explain the observed trends in the Caspian. Toxic loading can be seen as a negative input on each of the biological variables. In this case, although this diffuse negative input yields predictions that match with observed trends, the point here is that the contribution of the toxic load cannot be discerned as it is diffuse on all the variables but nutrients and because of that it cannot be distinguished from other negative inputs that are instead specifically defined as acting on single variables. The importance of the nutrient loading into the Caspian Sea could be assessed, both nutrient enrichment and toxic loading, by identifying points in time when nutrient loading into the system is known to be prevalent and its effect on the system hypothesised to be superior to other pressures, and taking in consideration the trends for the species trends within the same period, to analyse the effect that nutrient loading would have. A match within these conditions would clarify the importance of nutrients pressure in terms of its capacity to affect the system globally and to have played a role, even if within a limited timeframe, on the determination of the trends of the system. Although not a test on the effect that nutrient might have had in the system, from the model validity tests it came an alternative scenario for the trends in the Caspian Sea. In this scenario I considered the trend of nutrients in the system to be 0, that is, I considered the hypothesis of a possible stabilization of the nutrient levels in the Caspian Sea that some reports point to due to a higher control in toxic loading and nutrient enrichment in the Caspian by implementation of control laws and improvement of water treatment plants (results in ***Annex C – Complimentary analysis:***

Model validation). When I considered this hypothesis, the results improved by increase in one match for all the tests, with the best scenario being for concurrent negative pressures on seals, sturgeons and kilkas, for which a match between predictions and trends was obtained for 4 variables.

Building a graph for the structure of the interactions in the Caspian Sea was a challenging task. Model predictions needed to be validated through a comparison with observed changes in the level of the variables; these changes should be deduced from long term abundance trends. Such trends were not available for most of the variables that compose the Caspian Sea community: data found in the literature were inadequate to reproduce variations which should have been tested through a statistical analysis to assess significant variations along defined time intervals (Bodini et al. 2018). Most of the data were published in papers written in languages that are not in use in the scientific community and this precluded to exploit data efficiently to build up temporal trends. Lack of sufficient and clear data for multiple variables dictated that statistical analysis for trends development were not possible, and a general sense of a trend could not even be retrieved at all from the literature review for some variables. The timing of the input, that is the period of time in which perturbations acted on the system, could not be defined even with an acceptable approximation. Too vague were the indications in the literature about the occurrence of the perturbations. An in-depth analysis of the paths connecting the variables and the strength of interplay between them should be carefully taken into account in further analysis. In particular, the paths involving bony fish and kilkas should be studied in detail and a trend for phytoplankton and possible stresses involving this node should be considered.

Despite these setbacks some information could be taken and some hypothesis can be drawn to further studies: 1) bony fish and kilkas might play an important role in the system response to pressures, and therefore pressures on these species should be analysed in depth; 2) phytoplankton too seems to play an important role in the system, in particular a negative pressure on this variable produces one of the best rate of prediction and trends match, which points to its importance, and an hypothesis can be made that the water level instability in the early years of dam construction in the Volga might be the possible explanation for this negative input on phytoplankton, and therefore a further review of the literature should be made in order to verify it; 3) the high number of mismatches between predictions and trends, and the for some cases the prevalence of *0** signs in the predictions seems to indicate that the paths connecting the multiple variables of the system and their strength, and from there, the interactions strength between variables, seems to be of a high importance on the Caspian Sea. On a system where the importance of strength of interaction between nodes was low, trends would be easier explained with the results from table of predictions and further analysis, by contrast in a system where the interaction strength between variables and the paths connecting them as a higher importance, a study of the effects on inputs on a variable will have on the system where all interactions are ranked equally and path strength is simply determined by its length, the predictions outputted by the simulations will tend to fail more often; 4) from the lack of agreement of the predictions from concurrent inputs and the trends, it can be hypothesised that either the pressures did not occurred all at the same time, or their intensity was not the same, with some proving to overpower the others. The loop analysis algorithm does not allow to take in account the intensity of each pressure on the system, therefore a further analysis would have to rely on in-depth studies of multiple hypothetical scenarios of concurrent inputs drawn from the literature and of their results.

The major aim of this chapter was to build a reliable graph of the Caspian Sea network to explore the mechanisms behind the changes observed in the second part of the last century, in particular those involving kilkas, a major player of the system both for its economic and ecological importance. Due to the complexity of the system and the apparent importance that interaction strength plays in the systems response to pressures, it was impossible to give a conclusive answer to the questions posed for this chapter, instead we are left with more questions, in particular to the role interaction strength and paths strength play in the Caspian Sea. What became clear during this analysis is that the multiple pressures on the system might not have all occurred at the same time, even if their effects are seen concomitantly, and that a that a clear-cut answer on how a given pressure on the system will affect it cannot be provided without a complete understanding of how the system dynamics operate.

4.6. Annex A – Species trends

4.6.1. On data records

For the generation of the trends to be used as benchmarks to validate our model, a literature review was made. In this review we looked for data relative to either population biomass, numbers, or landing records (data used often as a proxy for fish population size), or when such data was not possible, literature statements over trends was also taken in consideration.

As stated in the main body of this paper, it wasn't possible to obtain such data on population size for all species, or even for those which some data was available, the records were not enough in order to construct a time series. Either way, data was present for most of the important species of our full-scale model of the Caspian Sea and then, for a good part of the nodes in our concatenated model, which was the one used for the analysis. In some cases, though, only a verbal declaration of the general direction of the trend was found. When necessary, a cross check between literature references was made in order to ascertain the general opinion on the literature over the trends in case.

Below follows a description of the trend obtained from the literature for each of the nodes in our analysis.

4.6.2. General fish landing trends

The landing records in the Caspian Sea have varied considerably in the past century. Changes in the sea level, dam constructions, increase in pollution and increase in fishing effort for most of the economic species as led to the observed variation in the landing records. Despite this variation across the last century, including during our period of analysis from 1950's to 1998, the record does show a steady decline in the total landing records in the Caspian Sea from the early 1970's until the end of 1990's, which can be interpreted as the landing records finally catching up with the real population trends of the multiple species fished in the Caspian Sea.

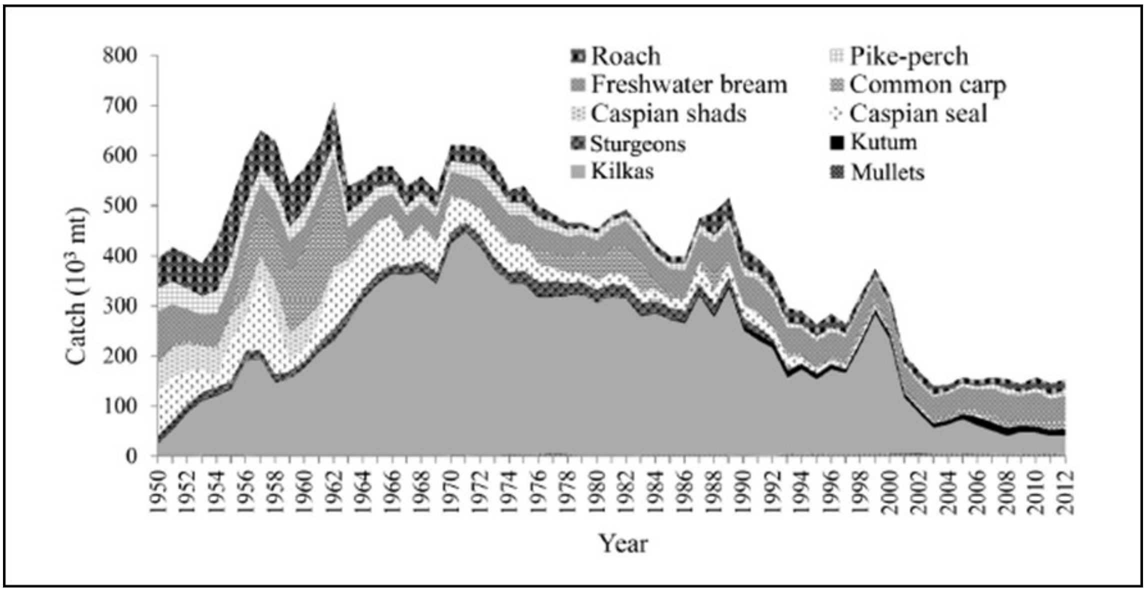


Figure 4.4: Catch dynamics of the Caspian Sea main species/ groups. Source: Fazli, Ghanghermeh, & Shahifar, 2017.

4.6.3.Species Trends

Seals

The Caspian Seal is the only aquatic mammal of the Caspian Sea, thus it has a great importance. Historical records point the existence of over a 1 million individuals in the early 20th century (CEP, 2007; Harkonen et al., 2012). During most of the past century, seals suffered from pressure from traditional seal pups hunting, which led its population to decline. The estimates for population size in 1989 vary between 128 and 400 thousand individuals (Harkonen et al., 2012). The Caspian Seal is currently considered an *Endangered species* in the IUCN Red List of Threatened Species (Goodman & Dmitrieva, 2016). From the literature we can ascertain that the Caspian Seals suffered a decline in its population levels across the past century and, therefore, we shall consider its trend to be negative, assigning it a “-“ value.

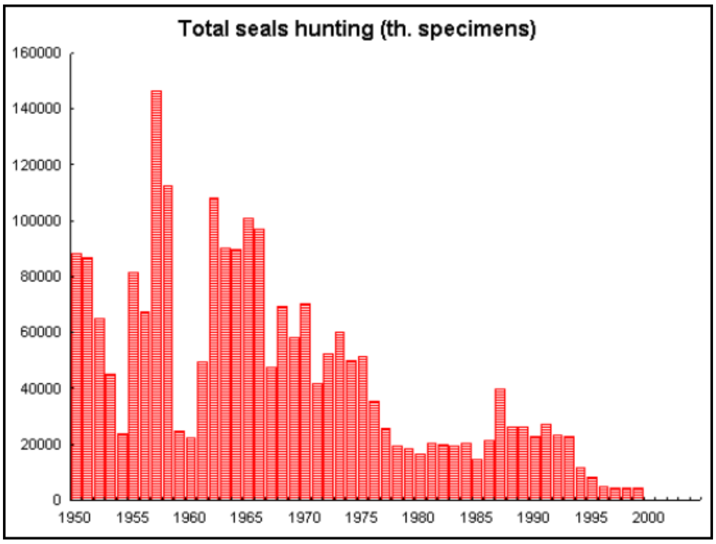


Figure 4.5: Total Seals hunting landing records from 1950 to 2000. Source CEP, 2007.

Sturgeons

The Caspian sturgeons accounted in the past for 80-90% of the total world caviar production. The effects of pollution and cut-off access to upper river spawning grounds have had a drastic effect in the population levels of the sturgeons, which are shown in the landing records, with a decline from 25 thousand tonnes in the early 1980's to 16.500 tonnes in 1990, to only 900 tonnes in 2004 (CEP, 2007; Kosarev & Yablonskaya, 1994). Once the major source of caviar in the world, almost all of the Caspian Sea sturgeon species have drastically declined as indicated by their status of Critically Endangered species, except for Sterlet Sturgeon which is ranked as Vulnerable in the IUCN Red Lis of Endangered Species (Gesner, Chebanov, & Freyhof, 2010; Gesner, Freyhof, & Kottelat, 2010b, 2010c, 2010a, 2010d; Qiwei, 2010). From the literature it is clear that the sturgeons of the Caspian Sea have been in decline through the past century, therefore in our analysis we will consider the sturgeons trend as negative and assign it a "-" value.

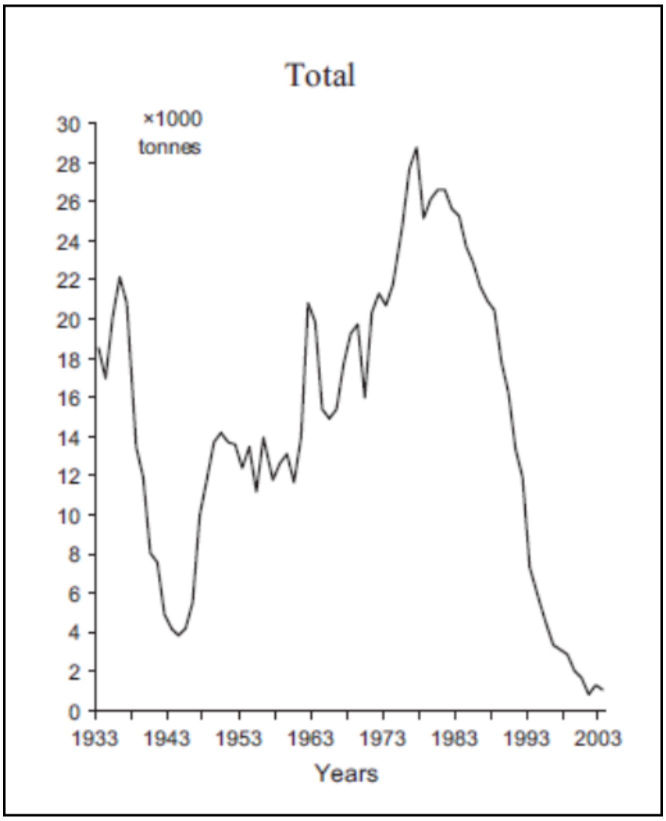


Figure 4.6: total landing records of sturgeons in the Caspian basin. Source: Ruban & Khodorevskaya, 2011

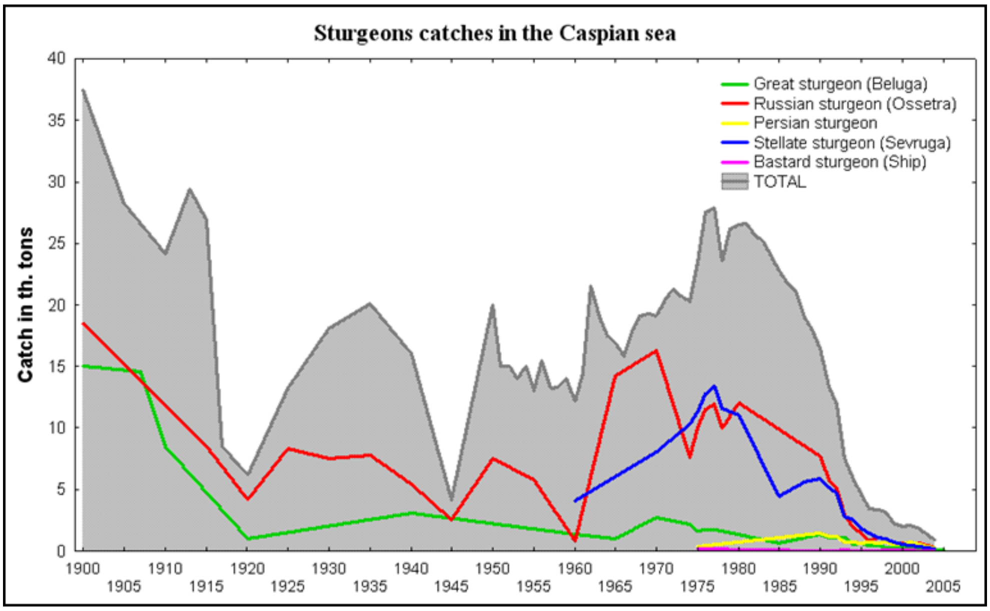


Figure 4.7: Total sturgeons landing records from 1900 until 2005. Source: CEP, 2007.

Bony fish

In our model a diverse group of species was considered under the umbrella of bony fish, e.g.: Wels catfish (*Silurus glanis*), European pikeperch (*Sander lucioperca*), Northern pike (*Esox luceus*), European bream (*Abramis brama*) and Roach (*Rutilus Rutilus caspicus*). Although a concise landing data for all the species considered under this group of species for the Caspian basin could not be retrieved from the literature, a clear picture could be taken for a general decline in the level of biomass of these species and of the group in general (Kosarev & Yablonskaya, 1994; UNEP, 2011). European bream landing peaked at more than 100 thousand tonnes in the early 1930s, experiencing a fall and stabilization over time at approximately 20 thousand annual tonnes. The Caspian roach experienced a decline from 167 thousand tonnes in 1935 to 20 thousand tonnes in 1996. European pikeperch saw a decline from 55 thousand tonnes in 1948 to 0.77 thousand tonnes in 1979, with only a slight increase afterwards, although the levels remained very low. From the trends retrieved from the literature we conclude that the population levels of the multiple species on this group were in decline for our period of analysis and therefore we will assume a negative trend and assign a "-" value.

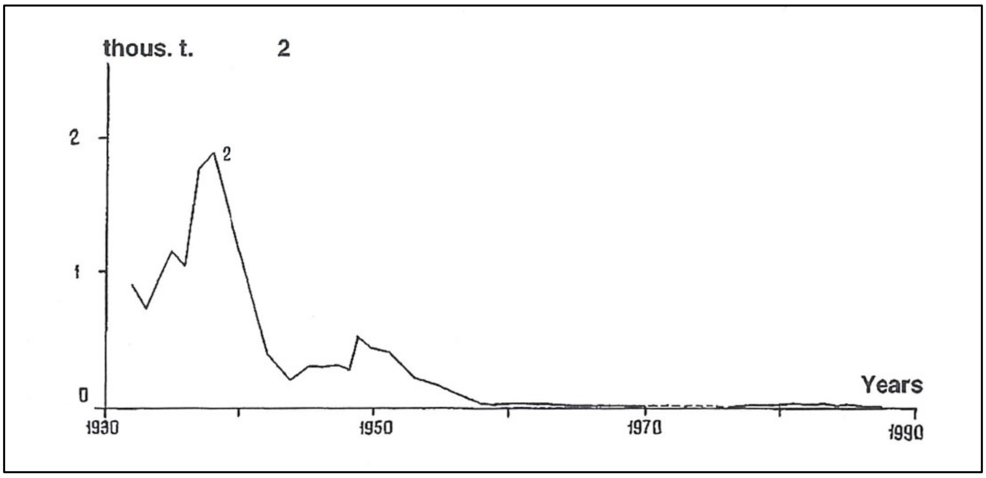


Figure 4.8: Dynamics of Salmon catches in the Caspian Sea. Source: Kosarev & Yablonskaya, 1994.

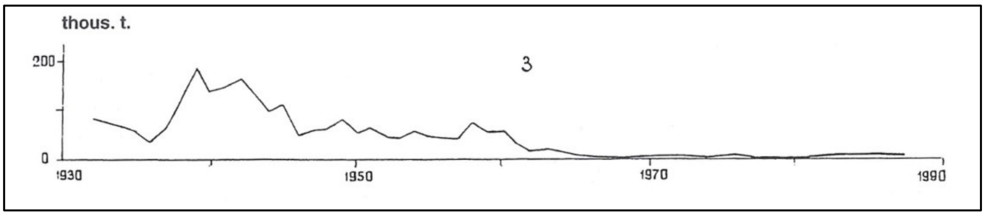


Figure 4.9: Dynamics of catches of Shads in the Caspian Sea. Source: Kosarev and Yablonskaya, 1994.

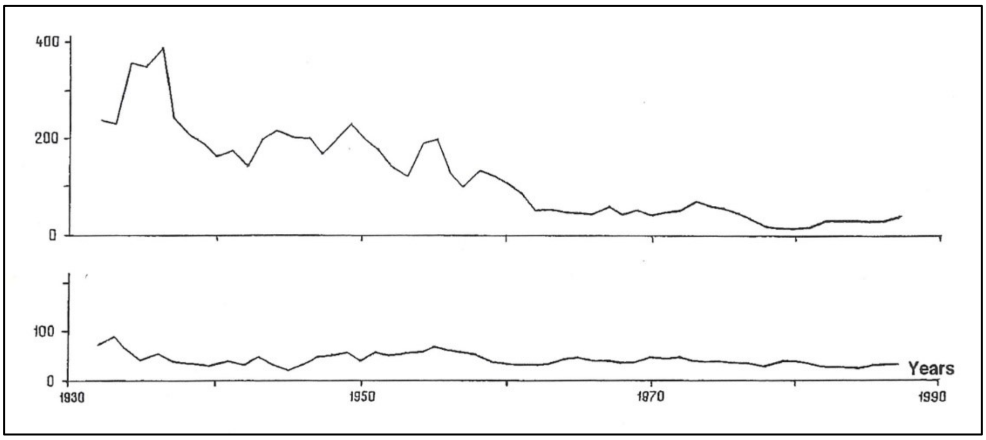


Figure 4.10: Dynamics of catches of semi-migratory (upper) and river fish (bottom) in the Caspian Sea. Source: Kosarev and Yablonskaya, 1994.

Kilkas

The Caspian kilkas are one of the most important species of this ecosystem, both for its economic importance for the populations around its shores, but also for its importance as a central node in the Caspian trophic chain. The kilkas fisheries has seen an increase in numbers from the 50s until the 70s due to increase in fishing efforts through an increase in the number of fishing vessels and implementation of improved fishing techniques that allowed for a higher yield. From the 70's onwards though, the numbers of landing started to decline, reflecting a possible decline in the population levels of the three species of Caspian kilkas (Mamedov, 2006). From the maximum landing records of 410 thousand tonnes in the 70's, the kilkas fishing industry declined to 132 thousand tonnes in 1996 (CEP, 2002; UNEP, 2011). This continuous decline in kilkas landing records, which saw only a brief recovery period in the late 90's is an indicator that the population levels of kilkas were in decline for our period of analysis and we will therefore assume a negative trend and assign a "-" value.

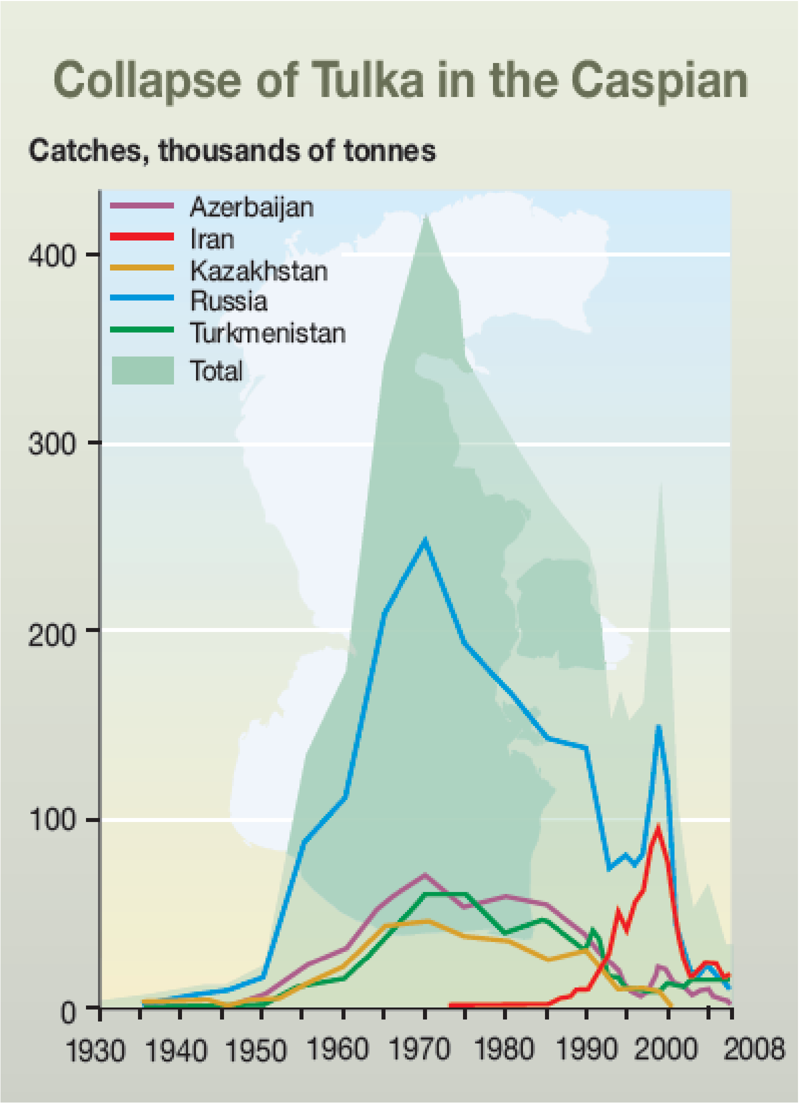


Figure 4.11: Total catches of kilkas in the Caspian Sea. Source: UNEP, 2011

Zooplankton, Phytoplankton, Benthic Organisms and Bacteria

Due to their economic importance, for most of the Caspian Sea fish species records of landing can be found, and from them trends for population levels can be derived, the same is not true for the primary and secondary producers of the system. For both zooplankton and phytoplankton exists gaps in their population records, with the date being multiple times presented using distinct units of measure and with conflicting records. This situation is aggravated by the fact that the population levels of both plankton groups present differences across the Caspian waters, and therefore the existing data is most often presented in relation to one of Caspian regions and not for the whole sea. The data presented for both phytoplankton and zooplankton is also limited to the year of 1986 in the best case, with records for the south Caspian for zooplankton ending almost one decade later, while those for the phytoplankton are limited to only 1976, with the southern records not being as complete as the other regions.

Some data exists for both zooplankton and phytoplankton in the late 90's, but since there is a great level of variability in the records shown, the difference between the last recorded data in the

80’s and the data on the 90’s can not be assumed as a trend, that is, an increase in the population levels between the late 80’s and late 90’s cannot be assumed as a positive trend, because since we don’t know the real story of the population, which might have actually risen during the first years of the 90’s and then be under a decline trend middle 90’s onwards until the present data, leading us to false conclusions.

In similar fashion, also for the benthic organisms and bacteria, the data is temporal limited until late 80’s, impairing our capacity to drawn trends for these groups.

As pointed out by multiple authors (CEP, 2002, 2007; H. J. Dumont, 1998), the recovery of data for the nodes of the lower trophic levels of the Caspian sea ecosystem is difficult. The access to original data is often impossible due to lack of source indication, or the source being in Russian or Arabic language. On top of this, the data that can be retrieved presents temporal gaps that makes it impossible to derive trends. And from written reports and notes it is also impossible to draw possible trends, since often there seem to be inconsistencies between authors.

For the reasons above, due to impossibility of drawing trends for the zoo- phytoplankton, benthic organisms and bacteria, trend signs won’t be assigned in our analysis for these nodes.

Nutrients

Before the damming of many of the subsidiary rivers of the Caspian Sea, in particular its main affluent, the Volga river in the North-Western part of the lake, the main source of nutrient to the sea came from its tributary rivers’ waters. The river damming, in special the Volga led to a decrease in the level of nutrients and pollutants reaching the Caspian waters. Even after the dam’s reservoirs have been filled and the water discharges were again regulated, the levels of nutrient import were still below that of previous times. After the 70’s though, with the increase of the agricultural industry and populations living in the lake shores, the levels of nutrient enrichment rose again due to runoff from agriculture and domestic waters, so much that it surpassed even the values observed in the pre-damming period (H. J. Dumont, 1998; UNEP, 2011). Taking this in consideration we will assume a positive trend and assign a “+” value.

4.7. Annex B – R code for simulations

Bellow follows the R code used for the simulations discussed in this chapter. For brevity, only the code and not the results are shown.

```
># loading of LevinsAnalysis package
>library(LevinsAnalysis)
># loading of the Caspian Sea models adjacency matrix
>caspian_c<-as.matrix(read.table("Caspian Net_C_v2.txt", header=T, sep="\t"))
>row.names(caspian_c)=colnames(caspian_c)
># signed digraph generation with user coordinates
>caspian_c_coord <- cbind(c(0,2,0,2,2,1,0,0,2),c(4,4,3,3,2,1,2,0,0))
>colnames(caspian_c_coord) <- c("x", "y")
>rownames(caspian_c_coord) <- c("Sl","St","Bo","Kk","Zoo","Phy","Bo","Bac","N")
```

```
>la_graph(J = caspian_c, fname = "caspian_c", layout_g = "user", coord =
caspian_c_coord, save_file = "pdf")
># stability tes
>cm_stability(caspian_c)
># computation of levins analysis algorithm
>caspian_lp <- levins_predictions(caspian_c, NT= 1112, fname= "caspian_c") #the
NT=1112 ensures for this matrix size a minimum of 10k random matrices creation
># models validation test
>caspian_press = as.list(rep(NA,1))
>Press_t1 <- cbind(c("-","-","-","-","+"),c("Sl","St","Bf","Kk","N"))
>caspian_press[[1]] <- Press_t1
>caspian_targ = matrix(c("-","-","-","-",NA, NA, NA, NA, "+"), nrow = 1, byrow =
TRUE)
>colnames(caspian_targ) <- c("Sl", "St", "Bf", "Kk", "Zoo", "Phy", "Bo", "Bac",
"N")
>caspian_mval <- model_validation(OUT_LP = caspian_lp, DF_list = caspian_press,
MV_target = caspian_targ, fname = "caspian_c")
>#    alternative pressure 1: overf only
>#    alternative pressure 2: overf only in Sl, St, Kk
>caspian_press_alt = as.list(rep(NA,2))
>Press_t2 <- cbind(c("-","-","-","-"),c("Sl","St","Bf","Kk"))
>Press_t3 <- cbind(c("-","-","-"),c("Sl","St","Kk"))
>caspian_press_alt[[1]] <- Press_t2
>caspian_press_alt[[2]] <- Press_t3
>caspian_targ_alt = matrix(c("-","-","-","-",NA, NA, NA, NA, "+","-","-","-","-
",NA, NA, NA, NA, "+" ), nrow = 2, byrow = TRUE)
>colnames(caspian_targ_alt) <- c("Sl", "St", "Bf", "Kk", "Zoo", "Phy", "Bo",
"Bac", "N")
>caspian_mval_alt <- model_validation(OUT_LP = caspian_lp, DF_list =
caspian_press_alt, MV_target = caspian_targ_alt, fname = "caspian_c_alt")
>#    alternative target: stabilization of N
>caspian_targ_alt_2 = matrix(c("-","-","-","-",NA, NA, NA, NA, "0"), nrow = 1,
byrow = TRUE)
>colnames(caspian_targ_alt_2) <- c("Sl", "St", "Bf", "Kk", "Zoo", "Phy", "Bo",
"Bac", "N")
>caspian_targ_alt_3 = matrix(c("-","-","-","-",NA, NA, NA, NA, "0","-","-","-","-
",NA, NA, NA, NA, "0" ), nrow = 2, byrow = TRUE)
>colnames(caspian_targ_alt_3) <- c("Sl", "St", "Bf", "Kk", "Zoo", "Phy", "Bo",
"Bac", "N")
>caspian_mval_alt_2 <- model_validation(OUT_LP = caspian_lp, DF_list =
caspian_press, MV_target = caspian_targ_alt_2, fname = "caspian_c_alt_2")
>caspian_mval_alt_3 <- model_validation(OUT_LP = caspian_lp, DF_list =
caspian_press_alt , MV_target = caspian_targ_alt_3, fname = "caspian_c_alt_3")
># strength interaction test and barplot generation
>caspian_sit <- sa_interaction_strength(OUT_LP = caspian_lp, NTS = 100, fname =
"caspian_c")
>barplot_sa_strength(OUT_SIS = caspian_sit, fname = "caspian_c")
># creation of ionterval matrices for interaction strength
>caspian_minv <- matrix(rep(0,(length(caspian_c))), nrow =
sqrt(length(caspian_c)))
>row.names(caspian_minv)=colnames(caspian_c)
>colnames(caspian_minv)=colnames(caspian_c)
>caspian_maxv <- matrix(rep(0,(length(caspian_c))), nrow =
sqrt(length(caspian_c)))
>row.names(caspian_maxv)=colnames(caspian_c)
>colnames(caspian_maxv)=colnames(caspian_c)
># value assignment for interaction strength intervals
>caspian_minv_st_bf<-edit(caspian_minv) #edit st-bf pair to 0.5
>caspian_minv_zoo_bf<-edit(caspian_minv) #edit zoo-bf pair to 0.5
>caspian_minv_bo_st<-edit(caspian_minv) #edit bo-st pair to 0.5
>caspian_minv_kk_zoo<-edit(caspian_minv) #edit kk-zoo pair to 0.5
```

```
>caspian_maxv_kk_st<-edit(caspian_maxv) # edit kk-st pair to 0.5
>caspian_minv_top_5<-edit(caspian_minv) #edit top 5 pair to 0.5
># computaiton of levins analysis algorithm with user defined intervals for
interaction strength
>caspian_lp_minv_st_bf <- levins_predictions(caspian_c, INT_MIN =
caspian_minv_st_bf, NT= 1112, fname= "caspian_c_min_st_bf")
>caspian_lp_minv_zoo_bf <- levins_predictions(caspian_c, INT_MIN =
caspian_minv_zoo_bf, NT= 1112, fname= "caspian_c_min_zoo_bf")
>caspian_lp_minv_bo_st <- levins_predictions(caspian_c, INT_MIN =
caspian_minv_bo_st, NT= 1112, fname= "caspian_c_min_bo_st")
>caspian_lp_minv_kk_zoof <- levins_predictions(caspian_c, INT_MIN =
caspian_minv_kk_zoo, NT= 1112, fname= "caspian_c_min_kk_zoo")
>caspian_lp_maxv_kk_st <- levins_predictions(caspian_c, INT_MAX =
caspian_maxv_kk_st, NT= 1112, fname= "caspian_c_max_kk_st")
>caspian_lp_minv_maxv_top_5 <- levins_predictions(caspian_c, INT_MIN =
caspian_minv_top_5, INT_MAX = caspian_maxv_kk_st, NT= 1112, fname=
"caspian_c_min_&_max_top_5")
># model validation test with intervals for top 5
>caspian_mval_alt_4 <- model_validation(OUT_LP = caspian_lp_minv_maxv_top_5,
DF_list = caspian_press, MV_target = caspian_targ, fname =
"caspian_c_alt_4_min_max_top_5")
># model validation test with intervals for top 5 alternative pressures
>caspian_mval_alt_5 <- model_validation(OUT_LP = caspian_lp_minv_maxv_top_5,
DF_list = caspian_press_alt, MV_target = caspian_targ_alt, fname =
"caspian_c_alt_5_min_max_top_5")
># model validation test with intervals for top 5 with alternate target
>caspian_mval_alt_6 <- model_validation(OUT_LP = caspian_lp_minv_maxv_top_5,
DF_list = caspian_press, MV_target = caspian_targ_alt_2, fname =
"caspian_c_alt_6_min_max_top_5")
># model validation test with intervals for top 5 alternative pressures and
alternative target
>caspian_mval_alt_7 <- model_validation(OUT_LP = caspian_lp_minv_maxv_top_5,
DF_list = caspian_press_alt, MV_target = caspian_targ_alt_3, fname =
"caspian_c_alt_7_min_max_top_5")
># computation of table of concurrent predictions
>#    concurrent predictions on seals pressure hypothesis 1: -Sl and -Kk
>Press_Sl_h1 <- cbind(c("-","-"),c("Sl","Kk"))
>levins_concurrent(caspian_c, DF = Press_Sl_h1, NT= 1112, fname =
"caspian_c_press_sl_h1")
>#    concurrent predictions on seals pressure hypothesis 2: -Sl, -Bf and -Kk
>Press_Sl_h2 <- cbind(c("-","-", "-"),c("Sl","Bf","Kk"))
>levins_concurrent(caspian_c, DF = Press_Sl_h2, NT= 1112, fname =
"caspian_c_press_sl_h2")
>#    concurrent predictions on seals pressure hypothesis 4: -Sl, -Bf, -Kk and
+N
>Press_Sl_h4 <- cbind(c("-","-","-","+"),c("Sl","Bf","Kk","N"))
>levins_concurrent(caspian_c, DF = Press_Sl_h4, NT= 1112, fname =
"caspian_c_press_sl_h4")
>#    concurrent predictions on seals pressure hypothesis 5: -Sl, -Bf
>Press_Sl_h5 <- cbind(c("-","-"),c("Sl","Bf"))
>levins_concurrent(caspian_c, DF = Press_Sl_h5, NT= 1112, fname =
"caspian_c_press_sl_h5")
>#    concurrent predictions on sturgeons pressure hypothesis 1: -St and -Bf
>Press_St_h1 <- cbind(c("-","-"),c("St","Bf"))
>levins_concurrent(caspian_c, DF = Press_St_h1, NT= 1112, fname =
"caspian_c_press_st_h1")
>#    concurrent predictions on sturgeons pressure hypothesis 1: -St and -Kk
>Press_St_h2 <- cbind(c("-","-"),c("St","Kk"))
>levins_concurrent(caspian_c, DF = Press_St_h2, NT= 1112, fname =
"caspian_c_press_st_h2")
```

```
>#    concurrent predictions on sturgeons pressure hypothesis 1: -St, -Bf and -
Kk
>Press_St_h3 <- cbind(c("-","-","-"),c("St","Bf","Kk"))
>levins_concurrent(caspian_c, DF = Press_St_h3, NT= 1112, fname =
"caspian_c_press_st_h3")
>#    concurrent predictions on sturgeons pressure hypothesis 1: -St, -Bf, -Kk
and +N
>Press_St_h6 <- cbind(c("-","-","-","+"),c("St","Bf","Kk","N"))
>levins_concurrent(caspian_c, DF = Press_St_h6, NT= 1112, fname =
"caspian_c_press_st_h6")
>#    concurrent predictions on sturgeons pressure hypothesis 1: -St, -Bo
>Press_St_h7 <- cbind(c("-","-"),c("St","Bo"))
>levins_concurrent(caspian_c, DF = Press_St_h7, NT= 1112, fname =
"caspian_c_press_st_h7")
>#    concurrent predictions on sturgeons pressure hypothesis 1: -St, -Bf, -Kk,
-Bo
>Press_St_h4 <- cbind(c("-","-","-","-"),c("St","Bf","Kk","Bo"))
>levins_concurrent(caspian_c, DF = Press_St_h4, NT= 1112, fname =
"caspian_c_press_st_h4")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf and -Kk
>Press_Bf_h1 <- cbind(c("-","-"),c("Bf","Kk"))
>levins_concurrent(caspian_c, DF = Press_Bf_h1, NT= 1112, fname =
"caspian_c_press_bf_h1")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf, -Kk and +N
>Press_Bf_h2 <- cbind(c("-","-","+"),c("Bf","Kk","N"))
>levins_concurrent(caspian_c, DF = Press_Bf_h2, NT= 1112, fname =
"caspian_c_press_bf_h2")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf and -Zoo
>Press_Bf_h3 <- cbind(c("-","-"),c("Bf","Zoo"))
>levins_concurrent(caspian_c, DF = Press_Bf_h3, NT= 1112, fname =
"caspian_c_press_bf_h3")
<#    concurrent predictions on bony fish pressure hypothesis 1: -Bf and +Zoo
>Press_Bf_h4 <- cbind(c("-","+"),c("Bf","Zoo"))
>levins_concurrent(caspian_c, DF = Press_Bf_h4, NT= 1112, fname =
"caspian_c_press_bf_h4")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf and -Phy
>Press_Bf_h5 <- cbind(c("-","-"),c("Bf","Phy"))
>levins_concurrent(caspian_c, DF = Press_Bf_h5, NT= 1112, fname =
"caspian_c_press_bf_h5")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf and +Phy
>Press_Bf_h6 <- cbind(c("-","+"),c("Bf","Phy"))
>levins_concurrent(caspian_c, DF = Press_Bf_h6, NT= 1112, fname =
"caspian_c_press_bf_h6")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf, -Zoo and -
Phy
>Press_Bf_h7 <- cbind(c("-","-","-"),c("Bf","Zoo","Phy"))
>levins_concurrent(caspian_c, DF = Press_Bf_h7, NT= 1112, fname =
"caspian_c_press_bf_h7")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf, +Zoo and
+Phy
>Press_Bf_h8 <- cbind(c("-","+","+"),c("Bf","Zoo","Phy"))
>levins_concurrent(caspian_c, DF = Press_Bf_h8, NT= 1112, fname =
"caspian_c_press_bf_h8")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf, -Zoo and
+Phy
>Press_Bf_h9 <- cbind(c("-","-","+"),c("Bf","Zoo","Phy"))
>levins_concurrent(caspian_c, DF = Press_Bf_h9, NT= 1112, fname =
"caspian_c_press_bf_h9")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf, +Zoo and -
Phy
>Press_Bf_h10 <- cbind(c("-","+","-"),c("Bf","Zoo","Phy"))
```

```
>levins_concurrent(caspian_c, DF = Press_Bf_h10, NT= 1112, fname =
"caspian_c_press_bf_h10")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf, -Sl
>Press_Bf_h11 <- cbind(c("-","-"),c("Bf","Sl"))
>levins_concurrent(caspian_c, DF = Press_Bf_h11, NT= 1112, fname =
"caspian_c_press_bf_h11")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf, -St
>Press_Bf_h12 <- cbind(c("-","-"),c("Bf","St"))
>levins_concurrent(caspian_c, DF = Press_Bf_h12, NT= 1112, fname =
"caspian_c_press_bf_h12")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf, -Sl and -
St
>Press_Bf_h13 <- cbind(c("-","-","-"),c("Bf","Sl","St"))
>levins_concurrent(caspian_c, DF = Press_Bf_h13, NT= 1112, fname =
"caspian_c_press_bf_h13")
>#    concurrent predictions on bony fish pressure hypothesis 1: -Bf, -Sl, -St
and -Kk
>Press_Bf_h14 <- cbind(c("-","-","-","-"),c("Bf","Sl","St","Kk"))
>levins_concurrent(caspian_c, DF = Press_Bf_h14, NT= 1112, fname =
"caspian_c_press_bf_h14")
>#    concurrent predictions on kilkas pressure hypothesis 1: -Kk and -Zoo
>Press_Kk_h1 <- cbind(c("-","-"),c("Kk","Zoo"))
>levins_concurrent(caspian_c, DF = Press_Kk_h1, NT= 1112, fname =
"caspian_c_press_kk_h1")
>#    concurrent predictions on kilkas pressure hypothesis 2: -Kk and +Zoo
>Press_Kk_h2 <- cbind(c("-","+"),c("Kk","Zoo"))
>levins_concurrent(caspian_c, DF = Press_Kk_h2, NT= 1112, fname =
"caspian_c_press_kk_h2")
>#    concurrent predictions on kilkas pressure hypothesis 3: -Kk and -Phy
>Press_Kk_h3 <- cbind(c("-","-"),c("Kk","Phy"))
>levins_concurrent(caspian_c, DF = Press_Kk_h3, NT= 1112, fname =
"caspian_c_press_kk_h3")
>#    concurrent predictions on kilkas pressure hypothesis 4: -Kk and +Phy
>Press_Kk_h4 <- cbind(c("-","+"),c("Kk","Phy"))
>levins_concurrent(caspian_c, DF = Press_Kk_h4, NT= 1112, fname =
"caspian_c_press_kk_h4")
>#    concurrent predictions on kilkas pressure hypothesis 5: -Kk, -Zoo and -Phy
>Press_Kk_h5 <- cbind(c("-","-","-"),c("Kk","Zoo","Phy"))
>levins_concurrent(caspian_c, DF = Press_Kk_h5, NT= 1112, fname =
"caspian_c_press_kk_h5")
>#    concurrent predictions on kilkas pressure hypothesis 6: -Kk, +Zoo and +Phy
>Press_Kk_h6 <- cbind(c("-","+","+"),c("Kk","Zoo","Phy"))
>levins_concurrent(caspian_c, DF = Press_Kk_h6, NT= 1112, fname =
"caspian_c_press_kk_h6")
>#    concurrent predictions on kilkas pressure hypothesis 7: -Kk, +Zoo and -Phy
>Press_Kk_h7 <- cbind(c("-","+","-"),c("Kk","Zoo","Phy"))
>levins_concurrent(caspian_c, DF = Press_Kk_h7, NT= 1112, fname =
"caspian_c_press_kk_h7")
>#    concurrent predictions on kilkas pressure hypothesis 8: -Kk, -Zoo and +Phy
>Press_Kk_h8 <- cbind(c("-","-","+"),c("Kk","Zoo","Phy"))
>levins_concurrent(caspian_c, DF = Press_Kk_h8, NT= 1112, fname =
"caspian_c_press_kk_h8")
>#    concurrent predictions on kilkas pressure hypothesis 9: -Kk and +N
>Press_Kk_h9 <- cbind(c("-","+"),c("Kk","N"))
>levins_concurrent(caspian_c, DF = Press_Kk_h9, NT= 1112, fname =
"caspian_c_press_kk_h9")
>#    concurrent predictions on kilkas pressure hypothesis 10: -Kk and -Sl
>Press_Kk_h10 <- cbind(c("-","-"),c("Kk","Sl"))
>levins_concurrent(caspian_c, DF = Press_Kk_h10, NT= 1112, fname =
"caspian_c_press_kk_h10")
>#    concurrent predictions on kilkas pressure hypothesis 11: -Kk and -St
```

```
>Press_Kk_h11 <- cbind(c("-","-"),c("Kk","St"))
>levins_concurrent(caspian_c, DF = Press_Kk_h11, NT= 1112, fname =
"caspian_c_press_kk_h11")
># concurrent predictions on kilkas pressure hypothesis 12: -Kk and -Bf
>Press_Kk_h12 <- cbind(c("-","-"),c("Kk","Bf"))
>levins_concurrent(caspian_c, DF = Press_Kk_h12, NT= 1112, fname =
"caspian_c_press_kk_h12")
># concurrent predictions on kilkas pressure hypothesis 13: -Kk, -Sl, -St and
-Bf
>Press_Kk_h13 <- cbind(c("-","-","-","-"),c("Kk","Sl","St","Bf"))
>levins_concurrent(caspian_c, DF = Press_Kk_h13, NT= 1112, fname =
"caspian_c_press_kk_h13")
># concurrent predictions on kilkas pressure hypothesis 14: -Kk, -Sl, -St, -
Bf and +N
>Press_Kk_h14 <- cbind(c("-","-","-","-","+"),c("Kk","Sl","St","Bf","N"))
>levins_concurrent(caspian_c, DF = Press_Kk_h14, NT= 1112, fname =
"caspian_c_press_kk_h14")
># concurrent predictions on nutrients pressure hypothesis 1: +N and -Sl
>Press_N_h1 <- cbind(c("+","-"),c("N","Sl"))
>levins_concurrent(caspian_c, DF = Press_N_h1, NT= 1112, fname =
"caspian_c_press_n_h1")
># concurrent predictions on nutrients pressure hypothesis 2: +N and -St
>Press_N_h2 <- cbind(c("+","-"),c("N","St"))
>levins_concurrent(caspian_c, DF = Press_N_h2, NT= 1112, fname =
"caspian_c_press_n_h2")
># concurrent predictions on nutrients pressure hypothesis 3: +N and -Bf
>Press_N_h3 <- cbind(c("+","-"),c("N","Bf"))
>levins_concurrent(caspian_c, DF = Press_N_h3, NT= 1112, fname =
"caspian_c_press_n_h3")
># concurrent predictions on nutrients pressure hypothesis 4: +N and -Kk
>Press_N_h4 <- cbind(c("+","-"),c("N","Kk"))
>levins_concurrent(caspian_c, DF = Press_N_h4, NT= 1112, fname =
"caspian_c_press_n_h4")
># concurrent predictions on nutrients pressure hypothesis 5: +N, -Sl, -St, -
Kk
>Press_N_h5 <- cbind(c("+","-","-","-"),c("N","Sl","Bf","Kk"))
>levins_concurrent(caspian_c, DF = Press_N_h5, NT= 1112, fname =
"caspian_c_press_n_h5")
```

4.8. Annex C – Complimentary analysis

4.8.1. Model Validation

Extra scenarios for model validation of the Caspian Sea model considering the stable trend in Nutrients:

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-94.563	66.935	69.432	7.432	-65.302	33.1	-53.541	53.541	12.239
-St	33.123	-96.873	25.493	1.038	-76.362	-63.948	88.566	-88.566	-25.166
-Bf	-5.915	-0.992	-98.763	98.157	4.725	1.178	0.478	-0.478	-0.548
-Kk	-70.715	-58.581	63.225	-98.833	56.878	-28.55	46.727	-46.727	-9.859
+N	63.272	80.772	55.828	-0.385	63.108	95.1	39.68	-39.692	95.03
mean	-14.96	-1.748	23.043	1.482	-3.391	7.376	24.382	-24.384	14.339
signs	0*	0*	?+	0*	0*	0*	?+	?-	0*
trend	-	-	-	-					0

Table 4.7: Prediction for the concurrent negative inputs on seals (-*Sl*), sturgeons (-*St*), bony fish (-*Bf*) and kilkas (-*Kk*) and positive input on nutrient (+*N*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-94.563	66.935	69.432	7.432	-65.302	33.1	-53.541	53.541	12.239
-St	33.123	-96.873	25.493	1.038	-76.362	-63.948	88.566	-88.566	-25.166
-Bf	-5.915	-0.992	-98.763	98.157	4.725	1.178	0.478	-0.478	-0.548
-Kk	-70.715	-58.581	63.225	-98.833	56.878	-28.55	46.727	-46.727	-9.859
mean	-34.518	-22.378	14.847	1.948	-20.015	-14.555	20.558	-20.558	-5.833
signs	?-	?-	0*	0*	?-	0*	?+	?-	0*
trend	-	-	-	-					0

Table 4.8: Prediction for the concurrent negative inputs on seals (-*Sl*), sturgeons (-*St*), bony fish (-*Bf*) and kilkas (-*Kk*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-94.563	66.935	69.432	7.432	-65.302	33.1	-53.541	53.541	12.239
-St	33.123	-96.873	25.493	1.038	-76.362	-63.948	88.566	-88.566	-25.166
-Kk	-70.715	-58.581	63.225	-98.833	56.878	-28.55	46.727	-46.727	-9.859
mean	-44.052	-29.506	52.717	-30.121	-28.262	-19.799	27.251	-27.251	-7.595
signs	?-	?-	+	?-	?-	0*	?+	?-	0*
trends	-	-	-	-					0

Table 4.9: Prediction for the concurrent negative inputs on seals (-*Sl*), sturgeons (-*St*) and kilkas (-*Kk*).

4.8.2.Concurrent Predictions

Seals

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-94.666	66.953	68.019	6.609	-65.213	31.447	-54.499	54.499	13.544
-Kk	-71.475	-58.024	62.43	-98.609	57.421	-28.224	47.356	-47.356	-11.572
mean	-83.07	4.465	65.225	-46	-3.896	1.611	-3.572	3.572	0.986
signs	-	0*	+	?-	0*	0*	0*	0*	0*

Table 4.10: Prediction for the concurrent negative inputs on seals (-*Sl*) and kilkas (-*Kk*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-95.004	66.028	68.2	4.786	-67.196	31.24	-52.136	52.136	13.075
-Bf	-7.308	-2.475	-98.996	98.342	4.623	-2.498	1.097	-1.097	0.514
mean	-51.156	31.777	-15.398	51.564	-31.287	14.371	-25.52	25.52	6.794
signs	-	?+	0*	+	?-	0*	?-	?+	0*

Table 4.11: Prediction for the concurrent negative inputs on seals (-*Sl*) and bony fish (-*Bf*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-94.5	67.443	68.941	5.933	-66.413	30.345	-55.436	55.436	16.723
-Bf	-5.957	-2.891	-98.76	98.151	2.984	0.035	2.025	-2.025	-2.61
-Kk	-70.884	-56.864	62.996	-98.642	58.783	-26.319	46.776	-46.776	-10.731
mean	-57.114	2.563	11.059	1.814	-1.549	1.354	-2.212	2.212	1.127
signs	-	0*	0*	0*	0*	0*	0*	0*	0*

Table 4.12: Prediction for the concurrent negative inputs on seals (-*Sl*), bony fish (-*Bf*) and kilkas (-*Kk*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-95.374	66.382	68.532	4.754	-63.906	32.601	-54.678	54.678	13.328
-Bf	-4.544	-2.815	-99.019	98.762	3.212	-1.904	2.441	-2.441	-0.502
-Kk	-70.354	-57.061	63.135	-98.785	58.042	-28.186	45.707	-45.707	-10.548
+N	62.691	79.909	56.676	-0.502	60.589	95.001	40.498	-40.498	94.977
mean	-26.895	21.604	22.331	1.057	14.484	24.378	8.492	-8.492	24.314
signs	?-	?+	?+	0*	0*	?+	0*	0*	?+

Table 4.13: Prediction for the concurrent negative inputs on seals (-*Sl*), bony fish (-*Bf*), kilkas (-*Kk*) and positive input on nutrients (+*N*).

Sturgeons

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-St	33.115	-96.819	25.117	1.356	-74.813	-64.85	87.909	-87.909	-23.152
-Bf	-5.285	-3.274	-99.181	98.503	1.123	-2.128	2.268	-2.268	-0.21
mean	13.915	-50.047	-37.032	49.929	-36.845	-33.489	45.089	-45.089	-11.681
signs	0*	-	?-	?+	?-	?-	?+	?-	0*

Table 4.14: Prediction for the concurrent negative inputs on sturgeons (-*St*) and bony fish (-*Bf*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-St	32.335	-96.982	26.182	-0.14	-74.825	-65.863	89.541	-89.541	-23.163
-Kk	-71.455	-56.996	64.319	-98.971	57.721	-27.632	45.391	-45.391	-9.265
mean	-19.56	-76.989	45.251	-49.556	-8.552	-46.748	67.466	-67.466	-16.214
signs	0*	-	?+	?-	0*	?-	+	-	0*

Table 4.15: Prediction for the concurrent negative inputs on sturgeons (-*St*) and kilkas (-*Kk*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-St	31.339	-96.786	25.405	-0.141	-73.939	-65.564	88.67	-88.67	-23.27
-Bf	-6.592	-3.143	-98.968	98.076	4.269	-1.173	2.545	-2.557	-0.844
-Kk	-71.194	-57.026	62.773	-98.733	56.24	-27.868	46.563	-46.563	-11.471
mean	-15.482	-52.318	-3.597	-0.266	-4.477	-31.535	45.926	-45.93	-11.862
signs	0*	-	0*	0*	0*	?-	?+	?-	0*

Table 4.16: Prediction for the concurrent negative inputs on sturgeons (-*St*), bony fish (-*Bf*) and kilkas (-*Kk*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-St	32.85	-96.419	27.63	-0.293	-74.254	-65.126	88.555	-88.555	-23.464
-Bf	-5.372	-3.242	-99.204	98.291	1.229	-3.171	0.293	-0.293	0.339
-Kk	-70.977	-57.028	63.862	-99.04	57.73	-25.711	47.431	-47.431	-13.329
+N	63.183	81.486	53.049	3.101	60.187	95.132	38.771	-38.771	95.038
mean	4.921	-18.801	11.334	0.515	11.223	0.281	43.763	-43.763	14.646
signs	0*	0*	0*	0*	0*	0*	?+	?-	0*

Table 4.17: Prediction for the concurrent negative inputs on sturgeons (-*St*), bony fish (-*Bf*), kilkas (-*Kk*) and positive input on nutrients (+*N*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-St	32.365	-96.235	26.601	1.15	-75.015	-65.322	87.519	-87.519	-21.883
-Bo	77.176	-38.222	74.178	1.336	10.75	85.567	-93.818	93.818	29.832
mean	54.77	-67.228	50.389	1.243	-32.133	10.122	-3.149	3.149	3.975
signs	+	-	+	0*	?-	0*	0*	0*	0*

Table 4.18: Prediction for the concurrent negative inputs on sturgeons (-*St*) and benthic organisms (-*Bo*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-St	33.473	-96.705	25.235	0.986	-75.125	-63.012	88.955	-88.955	-23.077
-Bf	-4.977	-2.378	-99.049	98.422	2.541	-3.539	1.497	-1.497	-0.569
-Kk	-71.528	-58.162	63.847	-98.817	58.046	-27.416	47.268	-47.279	-9.897
-Bo	78.141	-40.109	71.389	2.75	9.595	86.216	-94.338	94.338	28.553
mean	8.777	-49.338	15.355	0.835	-1.236	-1.938	10.846	-10.848	-1.248
signs	0*	?-	0*	0*	0*	0*	0*	0*	0*

Table 4.19: Prediction for the concurrent negative inputs on sturgeons (-*St*), bony fish (-*Bf*), kilkas (-*Kk*) and benthic organisms (+*Bo*).

Bony fish

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-6.996	-2.901	-99.275	98.409	2.176	-2.574	0.515	-0.515	0.842
-Kk	-69.911	-57.347	63.453	-98.76	58.259	-26.907	46.982	-46.982	-9.71
mean	-38.453	-30.124	-17.911	-0.175	30.218	-14.741	23.748	-23.748	-4.434
signs	?-	?-	0*	0*	?+	0*	?+	?-	0*

Table 4.20: Prediction for the concurrent negative inputs on bony fish (-*Bf*) and kilkas (-*Kk*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-5.889	-1.201	-98.927	98.741	3.02	-0.408	2.904	-2.904	-0.105
-Kk	-69.353	-57.714	63.755	-98.741	57.294	-27.627	43.883	-43.883	-10.134
+N	63.452	80.035	55.242	-0.362	61.399	94.682	40.875	-40.875	94.985
mean	-3.93	7.04	6.69	-0.121	40.571	22.216	29.221	-29.221	28.249
signs	0*	0*	0*	0*	?+	?+	?+	?-	?+

Table 4.21: Prediction for the concurrent negative inputs on bony fish (-*Bf*) and kilkas (-*Kk*) and positive input in nutrients (+*N*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-5.436	-5.436	-98.99	98.309	2.383	-3.605	0.951	-0.951	2.337
-Zoo	-53.035	-8.606	-45.638	-4.873	-95.844	73.042	77.175	-77.175	-88.024
mean	-29.235	-7.021	-72.314	46.718	-46.73	34.718	39.063	-39.063	-42.843
signs	?-	0*	-	?+	?-	?+	?+	?-	?-

Table 4.22: Prediction for the concurrent negative inputs on bony fish (-*Bf*) and zooplankton (-*Zoo*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-4.644	-3.283	-99.132	98.265	2.345	-1.266	1.618	-1.618	0.61
+Zoo	52.955	8.748	44.653	3.94	95.591	-73.734	-75.797	75.797	88.673
mean	24.155	2.732	-27.24	51.102	48.968	-37.5	-37.09	37.09	44.642
signs	?+	0*	?-	+	?+	?-	?-	?+	?+

Table 4.23: Prediction for the concurrent negative inputs on bony fish (-*Bf*) and a positive input on zooplankton (+*Zoo*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-6.494	-1.518	-99.299	98.388	0.327	-2.756	1.588	-1.588	-0.514
-Phy	-63.513	-79.911	-54.1	-2.523	-62.158	-94.487	-41.299	41.299	86.872
mean	-35.004	-40.715	-76.7	47.933	-30.916	-48.621	-19.855	19.855	43.179
signs	?-	?-	-	?+	?-	?-	0*	0*	?+

Table 4.24: Prediction for the concurrent negative inputs on bony fish (-*Bf*) and phytoplankton (-*Phy*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-6.273	-0.409	-99.112	97.921	2.628	-2.511	0.502	-0.502	0.899
+Phy	64.77	80.259	55.122	2.208	62.691	95.024	41.596	-41.596	-87.011
mean	29.248	39.925	-21.995	50.065	32.66	46.257	21.049	-21.049	-43.056
signs	?+	?+	?-	+	?+	?+	?+	?-	?-

Table 4.25: Prediction for the concurrent negative inputs on bony fish (-*Bf*) and positive input on phytoplankton (+*Phy*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-6.541	-2.663	-99.182	98.131	2.289	-0.888	1.378	-1.378	0.047
-Zoo	-54.263	-7.942	-44.055	-4.275	-95.959	73.744	76.197	-76.197	-89.045
-Phy	-63.63	-80.612	-54.613	-2.313	-62.088	-94.791	-39.851	39.851	87.737
mean	-41.478	-30.406	-65.95	30.514	-51.919	-7.312	12.575	-12.575	-0.42
signs	?-	?-	-	?+	-	0*	0*	0*	0*

Table 4.26: Prediction for the concurrent negative inputs on bony fish (-*Bf*), zooplankton (-*Zoo*) and phytoplankton (-*Phy*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-5.853	-1.175	-99.154	98.26	2.374	-2.351	2.045	-2.045	1.011
+Zoo	52.539	9.379	46.45	2.468	95.745	-73.296	-77.08	77.08	88.999
+Phy	63.517	80.254	54.584	0.682	61.777	95.369	40.809	-40.809	-87.941
mean	36.734	29.486	0.627	33.803	53.299	6.574	-11.409	11.409	0.69
signs	?+	?+	0*	?+	+	0*	0*	0*	0*

Table 4.27: Prediction for the concurrent negative inputs on bony fish (-*Bf*) and positive input on zooplankton (+*Zoo*) and phytoplankton (+*Phy*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-4.874	-4.897	-99.084	98.309	1.703	-1.28	3.464	-3.464	-0.928
-Zoo	-52.249	-6.518	-45.297	-2.736	-95.655	73.647	76.371	-76.371	-88.162
+Phy	64.674	79.918	55.349	1.632	60.869	94.974	41.844	-41.844	-87.316
mean	2.517	22.834	-29.677	32.402	-11.028	55.78	40.56	-40.56	-58.802
signs	0*	?+	?-	?+	0*	+	?+	?-	-

Table 4.28: Prediction for the concurrent negative inputs on bony fish (-*Bf*) and zooplankton (-*Zoo*) and positive input on phytoplankton (+*Phy*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-7.214	-0.58	-98.887	98.423	2.598	0.325	0.65	-0.65	-0.487
+Zoo	54.465	9	46.138	2.041	95.639	-73.684	-77.036	77.036	88.564
-Phy	-63.814	-80.817	-55.184	-0.742	-62.213	-95.106	-40.431	40.431	87.822
mean	-5.521	-24.132	-35.978	33.241	12.008	-56.155	-38.939	38.939	58.633
signs	0*	?-	?-	?+	0*	-	?-	?+	+

Table 4.29: Prediction for the concurrent negative inputs on bony fish (-*Bf*) and phytoplankton (-*Phy*) and negative input on zooplankton (+*Zoo*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-6.447	-3.3	-99.114	98.438	0.968	-3.416	0.082	-0.082	1.038
-Sl	-95.01	67.028	68.334	5.048	-64.603	35.758	-53.597	53.597	11.344
mean	-50.729	31.864	-15.39	51.743	-31.817	16.171	-26.758	26.758	6.191
signs	-	?+	0*	+	?-	0*	?-	?+	0*

Table 4.30: Prediction for the concurrent negative inputs on bony fish (-*Bf*) and seals (-*Sl*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-5.189	-3.02	-98.927	98.087	2.857	-4.093	1.061	-1.061	1.994
-St	32.991	-96.711	26.647	0.28	-74.904	-64.921	88.245	-88.245	-23.802
mean	13.901	-49.865	-36.14	49.184	-36.023	-34.507	44.653	-44.653	-10.904
signs	0*	?-	?-	?+	?-	?-	?+	?-	0*

Table 4.31: Prediction for the concurrent negative inputs on bony fish (-*Bf*) and sturgeons (-*St*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-5.973	-1.874	-98.929	98.533	3.272	-1.176	1.735	-1.735	0.221
-Sl	-95.203	66.678	68.075	4.622	-65.304	33.054	-52.87	52.87	11.328
-St	32.658	-96.67	25.998	-0.105	-74.083	-64.652	87.705	-87.705	-22.04
mean	-22.839	-10.622	-1.619	34.35	-45.372	-10.925	12.19	-12.19	-3.497
signs	?-	0*	0*	?+	?-	0*	0*	0*	0*

Table 4.32: Prediction for the concurrent negative inputs on bony fish (-*Bf*), seals (-*Sl*) and sturgeons (-*St*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Bf	-6.508	-2.916	-99.347	98.46	1.819	-1.889	2.251	-2.263	-0.84
-Sl	-95.101	66.55	67.786	4.945	-65.034	33.497	-55.004	55.004	13.972
-St	32.727	-96.921	26.545	0.676	-75.134	-65.337	89.153	-89.153	-23.046
-Kk	-70.842	-58.083	63.891	-99.114	58.642	-28.295	47.586	-47.586	-10.893
mean	-34.931	-22.843	14.719	1.242	-19.927	-15.506	20.997	-21	-5.202
signs	?-	?-	0*	0*	0*	0*	?+	?-	0*

Table 4.33: Prediction for the concurrent negative inputs on bony fish (-*Bf*),), seals (-*Sl*), sturgeons (-*St*) and kilkas (-*Kk*).

Kilkas

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-69.779	-57.788	63.097	-98.743	56.81	-27.823	46.1	-46.1	-9.686
-Zoo	-53.714	-8.801	-45.215	-3.423	-96.182	73.318	76.624	-76.624	-89.756
mean	-61.746	-33.294	8.941	-51.083	-19.686	22.747	61.362	-61.362	-49.721
signs	-	?-	0*	-	0*	?+	+	-	?-

Table 4.34: Prediction for the concurrent negative inputs on kilkas (-*Kk*) and zooplankton (-*Zoo*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-71.405	-59.433	62.757	-98.838	58.224	-28.653	46.623	-46.623	-11.147
+Zoo	54.458	5.661	45.879	2.011	95.629	-72.428	-76.613	76.613	88.33
mean	-8.474	-26.886	54.318	-48.413	76.927	-50.54	-14.995	14.995	38.591
signs	0*	?-	+	?-	+	-	0*	0*	?+

Table 4.35: Prediction for the concurrent negative inputs on kilkas (-*Kk*) and positive input on zooplankton (+*Zoo*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-71.054	-56.882	63.898	-98.978	57.138	-27.82	46.8	-46.8	-10.768
-Phy	-64.061	-79.556	-56.255	-0.221	-62.992	-95.145	-39.83	39.83	87.339
mean	-67.558	-68.219	3.822	-49.599	-2.927	-61.483	3.485	-3.485	38.285
signs	-	-	0*	?-	0*	-	0*	0*	?+

Table 4.36: Prediction for the concurrent negative inputs on kilkas (-*Kk*) and phytoplankton (-*Phy*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-70.376	-58.289	62.216	-98.737	58.312	-28.618	46.271	-46.271	-10.825
+Phy	63.526	79.939	55.506	1.192	61.913	94.435	40.402	-40.39	-86.86
mean	-3.425	10.825	58.861	-48.773	60.112	32.909	43.337	-43.331	-48.843
signs	0*	0*	+	?-	+	?+	?+	?-	?-

Table 4.37: Prediction for the concurrent negative inputs on kilkas (-*Kk*) and positive input on phytoplankton (+*Phy*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-71.379	-56.187	63.029	-98.748	57.231	-26.406	44.683	-44.683	-12.559
-Zoo	-53.52	-10.727	-44.776	-3.467	-96.544	72.121	76.76	-76.76	-87.916
-Phy	-63.841	-79.984	-54.958	-0.499	-63.168	-94.781	-39.974	39.974	87.313
mean	-62.913	-48.966	-12.235	-34.238	-34.16	-16.355	27.156	-27.156	-4.387
signs	-	?-	0*	?-	?-	0*	?+	?-	0*

Table 4.38: Prediction for the concurrent negative inputs on kilkas (-*Kk*), zooplankton (-*Zoo*) and phytoplankton (-*Phy*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-70.912	-56.638	63.611	-98.85	59.103	-26.775	44.9	-44.9	-9.379
+Zoo	54.056	9.766	45.346	3.205	95.868	-72.626	-77.11	77.11	88.215
+Phy	63.165	81.242	54.807	0.951	61.521	94.765	40.697	-40.697	-87.393
mean	15.436	11.457	54.588	-31.565	72.164	-1.545	2.829	-2.829	-2.852
signs	0*	0*	+	?-	+	0*	0*	0*	0*

Table 4.39: Prediction for the concurrent negative inputs on kilkas (-*Kk*) and positive input on zooplankton (+*Zoo*) and phytoplankton (+*Phy*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-71.695	-57.87	62.868	-98.716	57.286	-25.759	47.875	-47.875	-12.728
-Zoo	-52.405	-7.426	-45.446	-1.892	-96.544	73.05	76.6	-76.6	-87.996
+Phy	63.709	80.873	54.39	0.397	60.953	95.049	40.005	-40.005	-88.347
mean	-20.13	5.192	23.937	-33.404	7.232	47.447	54.827	-54.827	-63.024
signs	?-	0*	?+	?-	0*	?+	+	-	-

Table 4.40: Prediction for the concurrent negative inputs on kilkas (-*Kk*) and zooplankton (-*Zoo*) and positive input on phytoplankton (+*Phy*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-71.675	-56.86	64.71	-98.789	57	-25.786	46.168	-46.168	-12.439
+Zoo	53.086	7.035	45.097	2.702	95.365	-73.072	-75.868	75.868	88.26
-Phy	-63.382	-79.991	-54.321	-2.236	-60.354	-95.318	-39.879	39.879	87.282
mean	-27.324	-43.272	18.495	-32.774	30.67	-64.725	-23.193	23.193	54.368
signs	?-	?-	0*	?-	?+	-	?-	?+	+

Table 4.41: Prediction for the concurrent negative inputs on kilkas (-*Kk*) and phytoplankton (-*Phy*) and positive input on zooplankton (+*Zoo*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-70.17	-57.492	62.591	-98.795	58.674	-29.146	47.317	-47.317	-10.627
+N	63.936	80.971	56.542	0.498	64.121	95.202	39.39	-39.39	95.202
mean	-3.117	11.74	59.567	-49.148	61.397	33.028	43.353	-43.353	42.288
signs	0*	0*	+	?-	+	?+	?+	?-	?+

Table 4.42: Prediction for the concurrent negative inputs on kilkas (-*Kk*) and positive input on nutrients (+N).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-71.615	-57.271	63.392	-98.622	56.22	-28.513	46.011	-46.011	-11.272
-Sl	-94.417	66.92	68.835	4.754	-64.747	33.115	-53.604	53.592	13.725
mean	-83.016	4.825	66.114	-46.934	-4.264	2.301	-3.796	3.79	1.226
signs	-	0*	+	?-	0*	0*	0*	0*	0*

Table 4.43: Prediction for the concurrent negative inputs on kilkas (-*Kk*) and seals (-*Sl*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-71.218	-58.444	64.889	-98.781	57.131	-28.161	47.217	-47.217	-10.278
-St	33.224	-96.578	26.474	0.223	-75.741	-64.655	88.351	-88.351	-22.724
mean	-18.997	-77.511	45.681	-49.279	-9.305	-46.408	67.784	-67.784	-16.501
signs	0*	-	?+	?-	0*	?-	+	-	0*

Table 4.44: Prediction for the concurrent negative inputs on kilkas (-*Kk*) and sturgeons (-*St*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-71.124	-57.552	63.613	-98.736	54.885	-26.922	45.314	-45.314	-10.752
-Bf	-4.388	-3.826	-99.134	98.292	4.341	-1.907	2.001	-2.001	0.433
mean	-37.756	-30.689	-17.761	-0.222	29.613	-14.415	23.657	-23.657	-5.16
signs	?-	?-	0*	0*	?+	0*	?+	?-	0*

Table 4.45: Prediction for the concurrent negative inputs on kilkas (-*Kk*) and bony fish (-*Bf*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-70.239	-56.105	63.475	-99.02	58.274	-26.577	47.172	-47.172	-11.673
-Sl	-94.892	66.274	68.816	4.187	-62.589	32.525	-53.726	53.726	12.373
-St	33.085	-96.851	25.038	1.878	-75.837	-64.525	89.155	-89.155	-24.362
-Bf	-4.187	-2.577	-98.95	98.087	3.23	-1.668	0.431	-0.431	0.991
mean	-34.058	-22.315	14.595	1.283	-19.23	-15.061	20.758	-20.758	-5.668
signs	?-	?-	0*	0*	0*	0*	?+	?-	0*

Table 4.46: Prediction for the concurrent negative inputs on kilkas (-*Kk*), seals (-*Sl*), sturgeons (-*St*) and bony fish (-*Bf*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Kk	-70.478	-57.572	62.299	-98.795	59.101	-27.355	46.681	-46.681	-10.833
-Sl	-95.505	67.628	69.297	4.414	-64.801	35.28	-54.026	54.026	11.806
-St	34.561	-96.964	26.127	0.962	-75.715	-64.268	88.877	-88.877	-23.671
-Bf	-6.732	-4.206	-99.235	98.285	3.14	-3.372	1.425	-1.425	0.753
+N	63.805	79.84	54.188	2.213	61.858	94.694	41.096	-41.096	94.694
mean	-14.87	-2.255	22.535	1.416	-3.283	6.996	24.811	-24.811	14.55
signs	0*	0*	?+	0*	0*	0*	?+	?-	0*

Table 4.47: Prediction for the concurrent negative inputs on kilkas (-*Kk*), seals (-*Sl*), sturgeons (-*St*) and bony fish (-*Bf*) and positive input on nutrients (+*N*).

Nutrients

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
+N	64.183	81.293	55.921	0.106	62.939	94.742	40.43	-40.43	95.376
-Sl	-94.742	67.21	69.276	1.49	-64.488	32.285	-53.761	53.761	13.367
mean	-15.279	74.251	62.599	0.798	-0.774	63.514	-6.666	6.666	54.372
signs	0*	+	+	0*	0*	+	0*	0*	+

Table 4.48: Prediction for the concurrent positive inputs on nutrient (-*N*), and negative input on seals (-*Sl*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
+N	62.315	80.946	53.235	2.94	61.844	95.06	40.767	-40.767	94.895
-St	34.251	-96.589	26.817	0.118	-74.571	-65.232	88.215	-88.215	-20.63
mean	48.283	-7.822	40.026	1.529	-6.363	14.914	64.491	-64.491	37.133
signs	?+	0*	?+	0*	0*	0*	+	-	?+

Table 4.49: Prediction for the concurrent positive input on nutrient (-*N*), and negative input on sturgeons (-*St*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
+N	64.904	80.5	56.165	-0.337	63.579	95.142	41.336	-41.336	95.816
-Bf	-4.614	-4.172	-99.279	98.21	5.497	-2.684	0.383	-0.383	1.732
mean	30.145	38.164	-21.557	48.936	34.538	46.229	20.86	-20.86	48.774
signs	?+	?+	?-	?+	?+	?+	?+	?-	?+

Table 4.50: Prediction for the concurrent positive input on nutrient (-*N*), and negative input on bony fish (-*Bf*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
+N	63.9	80.301	54.051	1.97	62.233	94.708	39.585	-39.585	94.428
-Kk	-70.649	-57.035	64.075	-98.951	55.053	-27.218	45.798	-45.798	-11.621
mean	-3.375	11.633	59.063	-48.49	58.643	33.745	42.692	-42.692	41.404
signs	0*	0*	+	?-	+	?+	?+	?-	?+

Table 4.51: Prediction for the concurrent positive input on nutrient (-*N*), and negative input on kilkas (-*Kk*).

4.8.3.Interaction Strength

Tables of predictions tests using user-defined interaction strengths for specific variable pairs:

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
Sl	+	-	-	0*	+	?-	+	-	0*
St	?-	+	-	?+	+	+	-	+	?+
Bf	0*	0*	+	-	0*	0*	0*	0*	0*
Kk	+	+	-	+	-	?+	?-	?+	0*
Zoo	+	0*	?+	0*	+	-	-	+	+
Phy	+	+	?+	0*	+	+	?+	?-	-
Bo	-	?+	-	0*	0*	-	+	-	?-
Bac	?-	+	?-	?+	?+	?+	+	+	+
N	+	+	?+	0*	+	+	?+	?-	+

Table 4.52: Table of predictions with constrain on the interaction strength of sturgeon to bony fish link [*Sl -o Bf*] to a minimum value of 0.5.

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
Sl	+	-	-	0*	+	?-	+	-	0*
St	?-	+	0*	0*	+	+	-	+	?+
Bf	0*	0*	+	-	0*	0*	0*	0*	0*
Kk	+	?+	-	+	-	?+	?-	?+	0*
Zoo	?+	0*	+	?-	+	-	-	+	+
Phy	+	+	+	0*	+	+	?+	?-	-
Bo	-	?+	-	0*	0*	-	+	-	?-
Bac	?-	+	0*	0*	+	?+	+	+	+
N	+	+	+	0*	+	+	?+	?-	+

Table 4.53: Table of predictions with constrain on the interaction strength of zooplankton to bony fish link [*Zoo* -> *Bf*] to a minimum value of 0.5.

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
Sl	+	-	-	0*	+	?-	+	-	0*
St	?-	+	?-	0*	+	+	-	+	?+
Bf	0*	0*	+	-	0*	0*	0*	0*	0*
Kk	+	+	-	+	-	?+	?-	?+	0*
Zoo	+	0*	?+	0*	+	-	-	+	+
Phy	+	+	+	0*	+	+	?+	?-	-
Bo	-	+	-	0*	0*	-	+	-	?-
Bac	?-	+	?-	0*	+	?+	+	+	+
N	+	+	+	0*	+	+	?+	?-	+

Table 4.54: Table of predictions with constrain on the interaction strength of benthic organisms to sturgeons link [*Bo* -> *St*] to a minimum value of 0.5.

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
Sl	+	-	-	0*	+	?-	+	-	0*
St	?-	+	?-	0*	+	+	-	+	?+
Bf	0*	?+	+	-	0*	0*	?-	?+	0*
Kk	+	?+	-	+	-	0*	?-	?+	0*
Zoo	+	0*	?+	0*	+	-	-	+	+
Phy	+	+	+	0*	+	+	?+	?-	-
Bo	-	?+	-	0*	0*	-	+	-	?-
Bac	?-	+	?-	0*	+	?+	+	+	+
N	+	+	+	0*	+	+	?+	?-	+

Table 4.55: Table of predictions with constrain on the interaction strength of kilkas to sturgeons link [*Kk* -> *St*] to a maximum value of 0.5.

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
Sl	+	-	-	0*	+	?-	+	-	0*
St	?-	+	?-	0*	+	+	-	+	?+
Bf	0*	0*	+	-	?+	0*	0*	0*	?+
Kk	+	+	-	+	-	+	?-	?+	0*
Zoo	+	0*	?+	0*	+	-	-	+	+
Phy	+	+	+	0*	+	+	?+	?-	-
Bo	-	?+	-	0*	0*	-	+	-	?-
Bac	?-	+	?-	0*	?+	?+	+	+	+
N	+	+	+	0*	+	+	?+	?-	+

Table 4.56: Table of predictions with constrain on the interaction strength of kilkas to zooplankton link [*Kk -> Zoo*] to a minimum value of 0.5.

Models validation tests using user-defined interaction strengths for the top 5 pairs of the analysis of interaction strength influence in predictions:

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-93.288	65.24	42.323	27.005	-65.264	32.494	-46.638	46.638	3.512
-St	33.309	-95.469	51.025	-24.464	-56.538	-63.85	83.867	-83.867	-18.566
-Bf	-9.361	-41.58	-99.76	98.562	-42.635	4.423	53.35	-53.35	-34.316
-Kk	-53.758	-9.313	91.37	-99.808	88.949	-29.162	-17.895	17.895	31.128
+N	60.254	86.384	43.282	8.282	57.449	92.641	41.292	-41.292	95.206
mean	-12.569	1.052	25.648	1.915	-3.608	7.309	22.795	-22.795	15.393
signs	0*	0*	?+	0*	0*	0*	?+	?-	0*
trends	-	-	-	-					+

Table 4.57: Prediction for the concurrent negative inputs on seals (-*Sl*), sturgeons (-*St*), bony fish (-*Bf*) and kilkas (-*Kk*) and positive input on nutrient (+*N*), using the strength interval constrains as defined above.

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-93.288	65.24	42.323	27.005	-65.264	32.494	-46.638	46.638	3.512
-St	33.309	-95.469	51.025	-24.464	-56.538	-63.85	83.867	-83.867	-18.566
-Bf	-9.361	-41.58	-99.76	98.562	-42.635	4.423	53.35	-53.35	-34.316
-Kk	-53.758	-9.313	91.37	-99.808	88.949	-29.162	-17.895	17.895	31.128
mean	-30.774	-20.28	21.239	0.324	-18.872	-14.024	18.171	-18.171	-4.561
signs	?-	?-	?+	0*	0*	0*	0*	0*	0*
trends	-	-	-	-					+

Table 4.58: Prediction for the concurrent negative inputs on seals (-*Sl*), sturgeons (-*St*), bony fish (-*Bf*) and kilkas (-*Kk*), using the strength interval constrains as defined above.

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-93.288	65.24	42.323	27.005	-65.264	32.494	-46.638	46.638	3.512
-St	33.309	-95.469	51.025	-24.464	-56.538	-63.85	83.867	-83.867	-18.566
-Kk	-53.758	-9.313	91.37	-99.808	88.949	-29.162	-17.895	17.895	31.128
mean	-37.912	-13.181	61.573	-32.422	-10.951	-20.173	6.445	-6.445	5.358
signs	?-	0*	+	?-	0*	?-	0*	0*	0*
trends	-	-	-	-					+

Table 4.59: Prediction for the concurrent negative inputs on seals (-*Sl*), sturgeons (-*St*) and kilkas (-*Kk*), using the strength interval constrains as defined above.

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-93.288	65.24	42.323	27.005	-65.264	32.494	-46.638	46.638	3.512
-St	33.309	-95.469	51.025	-24.464	-56.538	-63.85	83.867	-83.867	-18.566
-Bf	-9.361	-41.58	-99.76	98.562	-42.635	4.423	53.35	-53.35	-34.316
-Kk	-53.758	-9.313	91.37	-99.808	88.949	-29.162	-17.895	17.895	31.128
+N	60.254	86.384	43.282	8.282	57.449	92.641	41.292	-41.292	95.206
mean	-12.569	1.052	25.648	1.915	-3.608	7.309	22.795	-22.795	15.393
signs	0*	0*	?+	0*	0*	0*	?+	?-	0*
trends	-	-	-	-					0

Table 4.60: Prediction for the concurrent negative inputs on seals (-*Sl*), sturgeons (-*St*), bony fish (-*Bf*) and kilkas (-*Kk*) and positive input on nutrient (+*N*), using the strength interval constrains as defined above and alternative trend scenario (*N=0*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-93.288	65.24	42.323	27.005	-65.264	32.494	-46.638	46.638	3.512
-St	33.309	-95.469	51.025	-24.464	-56.538	-63.85	83.867	-83.867	-18.566
-Bf	-9.361	-41.58	-99.76	98.562	-42.635	4.423	53.35	-53.35	-34.316
-Kk	-53.758	-9.313	91.37	-99.808	88.949	-29.162	-17.895	17.895	31.128
mean	-30.774	-20.28	21.239	0.324	-18.872	-14.024	18.171	-18.171	-4.561
signs	?-	?-	?+	0*	0*	0*	0*	0*	0*
trends	-	-	-	-					0

Table 4.61: Prediction for the concurrent negative inputs on seals (-*Sl*), sturgeons (-*St*), bony fish (-*Bf*) and kilkas (-*Kk*), using the strength interval constrains as defined above and alternative trend scenario (*N=0*).

	Sl	St	Bf	Kk	Zoo	Phy	Bo	Bac	N
-Sl	-93.288	65.24	42.323	27.005	-65.264	32.494	-46.638	46.638	3.512
-St	33.309	-95.469	51.025	-24.464	-56.538	-63.85	83.867	-83.867	-18.566
-Kk	-53.758	-9.313	91.37	-99.808	88.949	-29.162	-17.895	17.895	31.128
mean	-37.912	-13.181	61.573	-32.422	-10.951	-20.173	6.445	-6.445	5.358
signs	?-	0*	+	?-	0*	?-	0*	0*	0*
trends	-	-	-	-					0

Table 4.62: Prediction for the concurrent negative inputs on seals (-*Sl*), sturgeons (-*St*), and kilkas (-*Kk*) and positive input on nutrient (+*N*), using the strength interval constrains as defined above and alternative trend scenario (*N=0*).

5. Qualitative modelling of social-ecological systems

Opportunities for the understanding of social-ecological systems using qualitative loop analysis

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5.1. Summary

The sustainable management of social-ecological systems (SESs) requires understanding the complex structure of relationships and feedback among ecosystems (with their resources) and human entities (e.g. users and governance organizations). A core challenge is combining isolated knowledge from different fields (e.g. ecology, sociology, economy and political science) to represent the most relevant variables and interactions. Therefore, the construction and analysis of models integrating ecological and human actors is crucial to describe the functioning of SESs. Qualitative modelling is ideal for studying the dependencies between humans and nature. In particular, the qualitative technique of loop analysis allows yielding predictions on the effect that press perturbations (e.g. increase of nutrients' load or market-based incentives) have on the response of all systems' variables. Different interaction types, scarce information about functional relationships among variables and uncertainties in the values of the parameters are the rule rather than exception when studying SESs. Accordingly, a tool that deals with such uncertainties is called for and qualitative loop analysis seem to be perfectly suitable to investigate SESs. Here we introduce the key aspects of loop analysis and compare it with other qualitative methods (i.e. Bayesian Belief Networks, BBNs; Causal Loop Diagrams, CLDs; and Fuzzy Cognitive Maps, FCMs). We discuss current applications to SESs and suggest potential methodological developments. We conclude that loop analysis is an effective tool to model SESs, but some limits exist: (1) difficulties to define the timing of changing conditions and their impact; (2) issues in the identification of the variables exposed to diffuse press perturbations; (3) lack of solutions to assess nonlinear relations. However, it requires simple information concerning the presence of interactions (and their sign) and is appropriate in the context of poor data availability, being thus useful to move the first steps for the integration of the three dimensions of sustainability.

Keywords: ecological networks; Levins loop analysis; resilience; social-ecological systems; sustainability

5.2. Introduction

Human societies and their well-being depend on the provision of goods and services from ecosystems (Haines-Young & Potschin, 2010). Healthy ecosystems respond to human needs by maintaining structure and functioning over time (Costanza & Mageau, 1999), and the conservation of biodiversity is crucial for preserving stability and productivity of natural systems (Stachowicz, Fried, & Whitlatch, 2002; Worm et al., 2006). However, biodiversity is deteriorating worldwide at unprecedented rates and such decline poses concerns on the sustainable supply of goods and services from ecosystems (Lotze et al., 2006). The increasing level of human-induced impacts (e.g. overexploitation of resources, introduction of alien species in non-native environments, chemical pollution, nutrient enrichment and Climate Change) threatens biodiversity in both aquatic and terrestrial systems and calls for the formulation of effective conservation practices. Classical strategies focused on single populations but failed in implementing successful schemes for sustainable management (Hilborn, 2007). They showed to be ineffective for protecting marine ecosystems from human-related pressures and led to the decline of fish stocks, thus impairing the provision of food and services to human populations. There is therefore the need of a shift from conventional single-species, single-goal practices to a global strategy in which the unit of management is the whole social-ecological system (SES). Such change in perspective corresponds to move towards ecosystem-based management (EBM). Long et al. (2015) highlighted that consensus around the meaning of EBM has to be attained to foster its application and identified fifteen key principles for the definition of EBM. Among these principles they included the modelling of interconnections between ecological, social and governance systems, which emphasizes how network analysis can be appropriate for the assessment of ecosystem health and EBM.

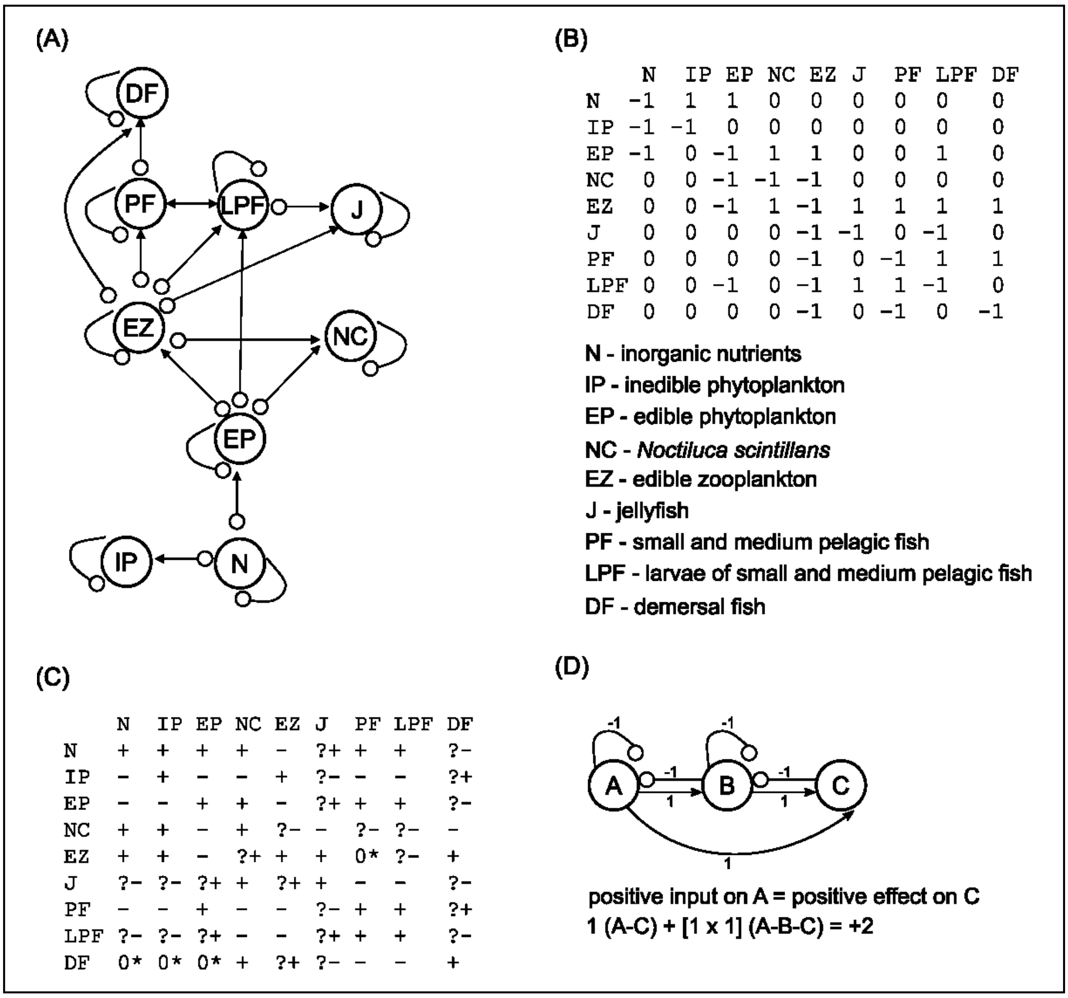
The adoption of the network perspective implies that the interactions that link variables belonging to the human and the ecological domains have to be concurrently taken into account, so that the SESs as a whole becomes the unit of management. The challenge is the identification of relationships at different hierarchical levels, which occur at various spatial and temporal scales. To facilitate integration Ostrom (2009) proposed a classificatory framework that describes the four essential dimensions of SESs: resource users, governance system, resource units and resource system. The relationships among these four dimensions occur at various geographical and temporal scales, within the rules defined by the ecological, social, economic and political settings. The choice of the suitable scales and the proper identification of the variables that constitute the SES and their connections are essential to assess under what conditions sustainability can be enhanced. Moreover, the concept of sustainability is multi-dimensional, and the spatial heterogeneity of SES variables can cause the mismatch between objectives that belong to either social or ecological domain. Indeed, the study of small-scale fisheries (SSFs) in the Mexican state of Baja California Sur showed the lack of association between different dimensions of sustainability (Leslie et al., 2015). Policies for the sustainable use of ecosystem goods and services require that the set of interactions linking ecological resilience (i.e. the adaptive capacity to withstand recurrent perturbations) to the society, the economy and the rules of governance (Hughes et al., 2005) be taken into account. This difficulty is witnessed and also enhanced by the adoption of strictly sectorial approaches: most studies about the social dimension of resource and environmental management mainly focused on social dynamics and treated the ecosystem as a black box; in parallel, the ecological approach to sustainability considered the social aspects only at the boundaries of the natural systems (Binder et al., 2013; Folke, 2006; Partelow et al., 2019). The balanced integration of social and ecological variables within the same modelling scheme is often precluded by: (1) difficulties in the identification of the most important interactions linking the variables; (2) missing details about the mathematical form of the interactions; (3) lack of qualitatively homogeneous data. Qualitative models represent an ideal tool to fill these gaps and due to simple application requirements (i.e. describing the presence of interactions and their sign) the algorithm of loop analysis (Richard Levins, 1968, 1974) can be used to concurrently consider the interactions in SESs among variables from different domains.

Loop analysis was developed to model the equilibrium levels of a system when growth rates of specific variables are altered by environmental variability. Methodologically loop analysis requires that only the sign of the relationships between the variables is specified. That is whether a variable positively or negatively affects another one. This simplicity overcomes the lack of quantitative information and simplifies the semantic conversion of the concepts related to the processes in which variables take part when belonging to different domains. Most of the works published so far focused on ecosystems and considered the human component as source of external perturbations. For example, Bodini et al. (2018) showed how overfishing affected the internal dynamics of the Black Sea but did not consider how socio-economic drivers inflated overfishing. Applications of loop analysis to SESs are taking ground (Dambacher et al., 2007; Martone et al., 2017). Here we show the potential of loop analysis for the integrative modelling of SESs. First, we introduce the methodological aspects behind the tool. Second, we discuss merits and limits of loop analysis for studying the dynamical behaviour of SESs. Then, we compare loop analysis with other qualitative methods that can be applied to SESs. Finally, we present ideas of possible methodological developments that could favour the diffusion of loop analysis in the context of SESs.

5.3. Loop analysis methodological aspects

Loop analysis is a qualitative technique for modelling complex systems as signed, directed graphs. Interactions are depicted as either positive or negative effects, but their strength is not specified (Figure 5.1a). Positive interactions are illustrated by arrow-headed links while negative interactions are visualized using circle-headed links. Any signed digraph has a matrix counterpart (adjacency matrix) in which positive (arrowheads) and negative (circle-heads) interactions are represented by the coefficients +1 and -1, respectively. Zeroes in the matrix stands for null direct relationships between variables (Figure 5.1b). The diagonal elements of the interaction matrix are self-effects on the variables and correspond to self-link in the graph (i.e. an arrowhead connecting one variable to itself) Loop analysis allows predicting how the variables respond to press perturbations that target specific variables. Press perturbations are forces that modify parameters in the variables' growth rates (Bender et al., 1984), such as warming that enhances the reproductive rate of jellyfish or ecolabels that increase the rate at which income of fishing cooperatives is produced. There are as many targets of press perturbations as the number of variables in the system (i.e. any variable can represent the entry point for press perturbations). Analysing the structural properties of the graph allows making predictions about the effect of press perturbations (Richard Levins, 1974, 1975).

The links in signed digraphs carry a direction (e.g., where the arrow and the circle point to). By following this direction one can identify paths that connect variables that can be far apart from one another in the system. With reference to Figure 5.1a nutrients (N) are connected to demersal fish (DM) by several paths, one of which is [N -> EP -> EZ -> PF -> DF]. Paths are the routes along which effects of press perturbations travels through the system. The effect of a path is positive or negative depending on the product of the signs of the links that compose the path.



(B)

	N	IP	EP	NC	EZ	J	PF	LPF	DF
N	-1	1	1	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	1	0
NC	0	0	-1	-1	-1	0	0	0	0
EZ	0	0	-1	1	-1	1	1	1	1
J	0	0	0	0	-1	-1	0	-1	0
PF	0	0	0	0	-1	0	-1	1	1
LPF	0	0	-1	0	-1	1	1	-1	0
DF	0	0	0	0	-1	0	-1	0	-1

N - **inorganic nutrients**
IP - **inedible phytoplankton**
EP - **edible phytoplankton**
NC - ***Noctiluca scintillans***
EZ - **edible zooplankton**
J - **jellyfish**
PF - **small and medium pelagic fish**
LPF - **larvae of small and medium pelagic fish**
DF - **demersal fish**

(C)

	N	IP	EP	NC	EZ	J	PF	LPF	DF
N	+	+	+	+	−	?+	+	+	?−
IP	−	+	−	−	+	?−	−	−	?+
EP	−	−	+	+	−	?+	+	+	?−
NC	+	+	−	+	?−	−	?−	?−	−
EZ	+	+	−	?+	+	+	0*	?−	+
J	?−	?−	?+	+	?+	+	−	−	?−
PF	−	−	+	−	−	?−	+	+	?+
LPF	?−	?−	?+	−	−	?+	+	+	?−
DF	0*	0*	0*	+	?+	?−	−	−	+

positive input on A = positive effect on C
1 (A-C) + [1 x 1] (A-B-C) = +2

Figure 5.1: Signed directed graph describing the Black Sea food web (a) and corresponding matrix of interactions (b) (Bodini et al., 2018). In the graph, positive interactions are denoted with arrow headed links while negative interactions are visualized with circle headed links. Names of all variables (i.e. nodes in the graph) are below the matrix of interactions. Loop analysis results for the Black Sea in the period 1960-1989 are summarized in the table of predictions (c). Additive and multiplicative rules are considered for predictions (the example here refers to a theoretical system with three variables) (d).

Next there is the feedback, which can be negative or positive. The former is a process in which an initial change in a variable gives rise to events that turn the variable back to its original value. A negative feedback, for example, occurs in agriculture when high agricultural yield reduces prices and so investments are cut, so that yield is reduced. The positive feedback occurs when an initial change gives rise to a chain of events that amplify the original change. For instance, during the period of the civil war in Colombia the level of violence displaced people from their land, and this contributed to further increase the level of violence. Because the feedback is "return effect" it originates when variables are linked by closed paths (e.g. circuits or loops) and they are negative or positive depending on the product of the signs of the links that form the loop (but see Puccia and Levins 1985, for a rigorous method to compute the feedback sign). In Figure 5.1d, for example the arrow from A to B and the circle headed link from B to A form a closed path, or loop, with negative feedback, because the product of the two links is negative. There can be circuits of different length depending on the number of variables linked together in a closed path. With these definitions we can express conceptually the algorithm of loop analysis (Puccia & Levins, 1985) and the sensitivity of a variable to a press perturbation depends on: a) whether the perturbation increases (+ sign) or decreases (- sign) the rate of change of the variable through which it enters the system; b) the sign of the path connecting the variable targeted by the press to the effect variable (the variable we want to predict its response); c) the sign of the feedback of the subsystem that remains when all variables on the path are ideally removed from the system (this is called complementary feedback); and d) the overall feedback, that is the feedback of the circuits that connect all the variables in the system. This algorithm can be summarized in the following formula:

$$\frac{\delta x_j}{\delta c} = \frac{\sum_{i,k} \left[\frac{\delta f_i}{\delta c}\right] \times \left[p_{ji}^{(k)}\right] \times \left[F_{n-k}^{(comp)}\right]}{F_n}$$

in which $[\partial f_i /\partial c]$ expresses whether the rate of change of the target variables (i) increases or decreases because of the changing parameter (c); $[p_{ji}^{(k)}]$,is the pathway to the response variable from the target variable, $[F_{n-k}^{(comp)}]$ is the complementary feedback and $[F_n]$ is the overall feedback. Summation occurs along all paths from the target variable to the effect variable

The complementary feedback can be envisioned as a reflecting barrier; if it is negative and strong, the more an impact is reflected back to the effect variable. If it is positive, then the effect variable changes in the opposite direction from the sign of the path. The overall feedback, the denominator of the formula, measures the resistance of the whole system to change. The responses can be positive (+, increase), negative (-, decrease) or null (0, no change) and are summarized in the table of predictions (Figure 5.1c). The convention is that effects generated by positive perturbations (those increasing the rate of change of the target variables) on row variables can be read along the columns. Consequences of negative perturbations are obtained by reversing the signs of the predictions.

For example, consider a positive press perturbation ($[\partial f_i /\partial c] > 0$) on node A (Figure 5.1d) if the focus is on the consequences that the press perturbation targeting A has on B , then the path is the positive link from A to B and the complementary subsystem is node C alone and in this case it does not form any circuit and the complementary feedback is null (i.e. equal to 0). The overall feedback is the feedback produced by the circuit that connects all the variables in the system (but see Puccia and Levins 1985 for further details). In the digraph of Figure 5.1d there is one single circuit connecting all the variables and includes three interactions by starting and ending with node A: [A $-oC - oB - oA$]; its sign is the product of the three negative links and thus it is negative.

In presence of graphs with many variables and interactions the number of paths between variables often increases, which leads to several null predictions (i.e. the number of positive paths equals that of negative paths). To deal with such ambiguities a simulation approach can be adopted, which introduces a random assignment of the magnitude to each and all the link coefficients. During simulations the coefficient intensities are taken from a uniform distribution in the interval]0, 1]. Only the matrices that satisfy the conditions of stability (i.e. those with the determinant different from zero and admitting matrix inversion) are accepted (Logofet, 1993). The elements of the inverse matrix show the net effect that press perturbations targeting the row variable x_i have on the column variable x_j. Such net effect is obtained by summing the contribution of impacts that diffuse through both direct links and all possible indirect pathways (Bender et al., 1984):

$$\frac{\partial \vec{x}^{*}}{\partial c_h} = (A_h)^{-1}\left(-\frac{\partial \vec{F}}{\partial c_h}\right)$$

$$if \quad \left(\frac{\partial \vec{F}}{\partial c_h} = +1\right) \quad then: \frac{\partial \vec{x}^{*}}{\partial c_h} = -(A_h)^{-1}$$

After n simulations an overall table of predictions is constructed by combining the z matrices that are stable and allow matrix inversion. For each stable matrix assembled using simulated interaction strengths, unambiguous responses in the table of predictions are generated (i.e. the signs are certain). The overall table of predictions is composed of symbols that depend on the percentages of signs from the various simulation runs. Hence, if the same entry in the tables of predictions from all z (stable) matrices yields the same sign (+ or -) then the expected direction of change is unambiguous. However, during simulations there are cases for which divergent predictions are recorded (i.e. depending on the random arrangement of interaction strength, the same element in the table of predictions can show either positive or negative sign). The conversion of the outcomes from each simulation run to symbols in the overall table of predictions depends on the percentages of positive (+) and negative (-) signs. The rules to move from simulations' results to the overall table of predictions are summarized in Table 2.1 from ***Chapter 2***.

5.4. Merits and limits of loop analysis to model SESs

Loop analysis is particularly suitable to investigate SESs. First, interconnections extend beyond the single domains, ecology, economy, societal and create complex wholes. After the Nile perch invaded Lake Victoria a dramatic restructuring of the ecological community took place, which, in turn, cascaded into deep societal and economic changes (Downing et al., 2014). To disentangle drivers and dynamics of change in such complex scenario, Downing and co-workers designed an eco-social qualitative model that traced connections across disciplinary boundaries.

Second, loop analysis educates intuition to cope with complexity. Often complex systems defy our predictions and effects of policies or management interventions are at best ineffective if not damaging (Richard Levins, 1995). This depends on the feedbacks that are produced by the linkages between the variables and that remain hidden to our comprehension if complexity does not become our central intellectual issue. Cinner (2011), by discussing problems of the reef fishery, emphasizes that the feedback between social and ecological variables may create social-ecological traps (e.g. situations when feedbacks between social and ecological systems lead toward an undesirable state that may be difficult or impossible to reverse): these phenomena are extremely interesting to be explored by loop analysis which, by disentangling feedbacks loops, helps making the arcane obvious. This opportunity, however, cannot be fully exploited if the feedback structure of the systems is not adequately represented and the relationships between the variables remain mostly unidirectional as it may occur when social and environmental variables are incorporated in a unique model (J. M. Dambacher et al., 2007).

Third, loop analysis proposes a rigorous approach to diagnosis. Increasingly, diagnostic approaches are requested in the analysis of SESs to causally understand the multiple outcomes that can arise from the interaction of different system attributes (Kittinger et al., 2013). The table of predictions, the main outcome of loop analysis, allows disentangling causative mechanisms by linking correlation patterns, source of change and network structure (Bodini & Clerici, 2016; Bodini et al., 2018). For any entry point of press perturbation (any row in the table of predictions, see Figure 5.1c) variables are predicted to change so that correlation patterns among them emerge. By comparing such patterns with observed changes in the level of the variables one can identify which component is affected by external drivers and find the cause and effects mechanisms responsible for those changes as due to the linkage structure.

Fourth, loop analysis incorporates external drivers as inputs to the rate of change of the variables. External drivers, both social and biophysical, have been described as playing an important role in SESs dynamics (Kittinger et al., 2013). In Baja California, Mexico, for example, climate-driven hypoxia caused mortality in marine species with limited mobility, resulting in declines in stocks targeted by small scale local fisheries, which, in turn, may have caused small-scale fishers to switch fishing effort toward less-affected species (Micheli et al., 2012). This effect was explored in a scenario analysis using qualitative loop analysis (Martone et al., 2017) a predicted large scale consequences of this environmentally external driver.

The intuitive visualization of the entities and the interactions among them is suitable to accommodate the general framework proposed by Ostrom (2009) for analysing the sustainability of SESs. Each node in the digraph can be one of the four elements (i.e. core subsystems: governance system, resource users, resource system, and resource units) and either positive or negative links can visualize their direct relationships. So far, the main focus has been dedicated to the visualization of ecological variables and interactions, and the inclusion of social-economic aspects have been treated as external to the system (Carey et al., 2013; Espinoza-Tenorio et al., 2013; Reum et al., 2015). The simple graphical format that constitutes the input for the loop analysis facilitates the participation of all stakeholders to model construction. Although most of the current applications adopted a top-down approach to embed management strategies in the models (i.e. literature data were consulted for defining the interactions) the study of Espinoza-Tenorio et al. (2013) presents a valid alternative. In this work both quantitative and qualitative information regarding the biological and social aspects of fisheries dynamics and management were retrieved using structured interviews with fishermen, participatory research, key informant interviews, and workshops.

However, some limits should be taken into account. Theoretically there are limitations that have already been discussed (Justus, 2006) and here we focus on those that matter with the use of loop analysis in studying SESs. First, there can be difficulties to define the timing of changing conditions and that of the system response to impacts. SESs are resilient and cope with continuous exposure to press perturbations according to adaptive dynamics principles (Folke, 2006; Hughes et al., 2005). It can therefore be complicated to identify whether the SESs reside in stable states or dynamically change their equilibrium. The exact moment at which the system responds to a press perturbation cannot be detected with precision and the contribution of concomitant perturbations may further confound this detection.

Second, the variables of SESs (e.g. resources and their users) can show asynchronous behaviour and heterogeneous geographical distribution (Leslie et al., 2015). Their optimization does not necessarily occur at the same temporal and spatial scale, an aspect that might remain overlooked when constructing graphs. The uneven geographical distribution of the actors might be addressed by including in the models different variables for the same type of user (e.g. various nodes that indicate the fishermen and their interactions in different regions). Third, there can be issues in the identification of the variables exposed to press perturbations (i.e. impacts of overfishing vs. Climate Change). While marketing solutions (e.g. the introduction of ecolabels) can be easily targeted to specific user groups (e.g. the members of fishing cooperatives; see Martone et al., 2017). Some press perturbations that act on the ecological subsystem can be more easily assigned to specific variables (e.g. nutrient enrichment takes the form of positive inputs on phytoplankton and overfishing targets the node of small and medium pelagics; see Bodini et al., 2018). Climate change (e.g. warmer winters) affects many components of the ecological system. One possible solution is prioritizing as press perturbation's targets the most responsive biological variables (e.g. jellyfish have faster blooming rates than expected from the body size; see Nival & Gorsky, 2001). Finally, loop analysis is problematic for assessing nonlinear relationships. Non-linearity can emerge by combining the impacts of pathways of different lengths. Longer pathways have lower intensity than shorter ones since the interaction strengths randomly assigned during the simulations are in the interval]0,1] (i.e. the intensity of each pathway is obtained by multiplying the strength of its constitutive links that have upper bound equal to 1). To avoid penalizing the impact of longer pathways simulations could be carried out by constraining the lower limit from which interaction strengths are randomly drawn during simulations (i.e. by setting the lower limits of some "strong" interactions closer to 1). As an alternative one could include non-linear functions to model those specific interactions that play crucial roles for the dynamics of the SES (e.g. by relying on previous literature data or results from specific experiments/surveys).

5.5. Comparison of loop analysis with other qualitative methods for SESs

SESs form complex networks of linkages and loop analysis is designed to qualitatively predict how variables that are embedded in SESs respond to policies and management interventions (e.g. introduction of new regulations for the exploitation of resources, market-based incentives and adoption of new marketing solutions as the ecolabels). A limited number of applications to investigate complex SES made use of the loop analysis, but the interest toward it is taking ground especially in the context of fishery (Anthony, Dambacher, Walshe, & Beeden, 2013; Carey et al., 2013; J. M. Dambacher, Rothlisberg, & Loneragan, 2015; Espinoza-Tenorio et al., 2013; Martone et al., 2017). This speaks about the potential of the method. One limitation of the loop analysis is that it predicts changes in the equilibrium level of the variables (Justus, 2006) but real systems are generally not at the equilibrium. Previous studies have however offered evidence that predictions from loop analysis apply successfully to changes in average values of the variables (Antonio Bodini, 2000). Average values should be long-term, but Bodini et al. (2018) showed that averages taken over either 5 or 10 years can be used to grasp variable responses to press perturbations. The appropriate time scale for taking averages, however, very much depends on the system under investigation.

Other qualitative modelling approaches can be used to study SESs. Fuzzy Cognitive Maps (FCMs) is one of these. It makes the magnitude of links explicit through a semi-quantification of the relationships that link the variables (Kok, 2009; Özesmi & Özesmi, 2004). The semi-quantification of the links may resolve the ambiguities typical of loop analysis about the net effect generated by the combination of contrasting pathways. Also, FCMs can make predictions about multiple simultaneous perturbations. Both the state of the variables (concepts, in the technical language of FCMs) and the strength of the links (edges between the concepts) are quantified assigning standardized values in the range [0, 1] for states and [-1, 1] for the links. Although these are relative values (i.e. each of them is assigned in relation to the others), some criteria for the quantification must be identified. These criteria must be supported by some knowledge about the level of the variables and interactions in the system, and in particular the use of FCMs seems appropriate when the estimates of variable state and link strength are the outcomes of either a combination of multiple FCMs from individual stakeholders or a set of values defined through participatory workshops. This imposes a certain level of knowledge about the system and it automatically selects the working groups among stakeholders that possess some previous knowledge about the system. It follows that FCMs cannot be public, reproducible and intelligible in the way that loop analysis is. Kok (2009) posits that vague or complex concepts such as “consumer behaviour” must not be taken into account when applying FCMs as guessing about their magnitude, is inherently difficult. In contrast, loop analysis allows including “awareness” in a malaria model (Yasuoka et al., 2014), “environmental attractiveness” in a tourism model (Bodini et al., 2000), and the “role of the unions” in a model on diabetes (Lewontin & Levins, 2007). In these aspects it seems that FCMs share the same limitations of quantitative models, as they tend to exclude factors that are difficult or impossible to measure, no matter if they play a recognized role in the dynamics of the system. The connections among the variables in FCMs are designed on the basis of fuzzy conditional (IF-THEN) statements that are of the type “if the level of variable A is high, that of variable B is low”. Thus, connections are deduced from correlations between the variables derived from observing the system (Stylios & Groumpos, 1999). However, Levins and Puccia (1988) pointed out that patterns of correlation depend on the network structure and the entry point of the perturbation. For example, any two variables may show positive correlation in response to a specific press perturbation but opposite correlation (or no correlation) in response to some other input. It follows that defining interactions between variables on the base of their correlations may be misleading. Both loop analysis and FCMs allow predicting changes in the level of the variables in a complex system following a perturbation to one of them. In loop analysis perturbations are changes in the parameter that governs the rate of change of the variables. For example, an increase in the mortality rate of a population triggered by a pollutant. FCMs instead consider perturbations as changes in the level of the variables. To predict, say, the impacts of a pollutant that affects a population, FCMs consider the change induced by the pollutant on the abundance of the target population as the initial event (i.e. the perturbation). Since the chemical pollutant is toxic more individuals will die in the unit time and the abundance of the target population will lower. Thus, the initial event is deduced from a more or less plausible linear sequence of steps. Indeed, this series of events overlooks the fact that the response of the target population to increased mortality is also mediated by the network of interactions with the other variables, which cannot be defined using common sense linear expectations. This leads to the circular argument that FCMs predict the effects given a cause that is in turn an effect that FCMs should predict. On the other hand, we can be confident that the pollutant increases the mortality rate of the target population, which is the initial event in loop analysis. Loop analysis considers the role of the environmental variability in changing the parameters that govern the growth rates of the variables and does not interpret it solely as the cause of variable fluctuations like FCMs do.

Other qualitative modelling approaches used in SESs include Causal Loop Diagrams (CLDs; Hanspach et al., 2014; Tenza et al., 2017) and Bayesian Belief Networks (BBNs; Borsuk et al., 2004; Pollino et al., 2007). CLDs make predictions by logically reconstructing the chains of causes and effects between the variables on the basis of link polarities (e.g. the signs of the directed links, that is the effects of one variable over the other). Predicting the behaviour of complex networks by identifying the feedback effects using link polarity is difficult and can lead to misleading interpretations (D. C. Lane, 2008; Richardson, 1997). Most problems originate from polarities. Consider, for example, the case in which the level of violence displaces people from rural areas and force them to move to the cities (Colombia is a paradigmatic example, Ibáñez and Vélez, 2008). The causal connections are that level of violence increases the migration rate which, in turn, increases the population level in the city. So, the higher the level of violence the greater the urban population. However, if the level of violence gets lower also the migration rate is reduced but this does not reduce the population in the city as it continues to increase unless an opposite migratory flux occurs. So major problems arise because variables can be stocks and rates and this confound the articulation of causal pathways (Sweeney & Sterman, 2007).

Similarly, specifying the relevant conditional probabilities as required by BBNs can be a laborious and time-consuming process (Marcot et al., 2001; Ticehurst et al., 2007). Moreover, to include feedback mechanisms via cyclic network structures requires dynamic time-explicit BBNs, which depend on extensive parameterization. Similar to FCMs, combining BBNs with loop analysis has great potential for improving predictions and model validation (Anthony et al., 2013; Melbourne-Thomas et al., 2012). However, it must be emphasized that these applications of BBNs are based on the signs derived from the analysis of the loop models. As such, their outcomes are contingent on the assumptions and limitations of the signed diagraph models.

Central for the understanding of the complex causality in SESs is our ability to diagram the relationships between the variables. Predictions are strongly dependent on the specific assumptions about the relevant components of the SESs, the nature of the linkages among these components, and the overall structure of the network. There is no recipe for modelling development, but great effort must be devoted to assimilation of facts, observations and hypotheses. Increasing the reliability of predictions can be possible by designing alternative graphs. This allows addressing uncertainty about the system structure and determining which differences matter. Robust outcomes may be the effect of a core structure common to all models upon which few links added or removed cannot change radically the predictions. The core structure represents the fundamental backbone composed of more certain variables and interactions. Disagreements among stakeholders, scientists or managers, do not limit the application of loop analysis; rather, they offer the opportunity to involve stakeholders in a participatory model construction (Anthony et al., 2013) where different types of system's knowledge can be used to determine variables and links that may be important to further examine (Stier et al., 2017). The adoption of such a comprehensive, system-wide approach aims to formulate management strategies that reconcile ecological integrity, intergenerational opportunities, and economic efficiency, three key dimensions of the sustainable development paradigm.

5.6. Possible development for the application of loop analysis to SESs

Making predictions is difficult, especially when we face the uncertainty associated with new, unknown events, changing dynamics and lack of quantitative data. This is the case for example of Climate Change, which produces completely new phenomena and dynamics. An adaptive management approach that allows for continually assessing new evidence as understanding has been called for. We believe that in the new scenarios that we are facing, the method of loop analysis can be helpful. It has the necessary adaptability to be used in changing contexts: when in doubt about critical linkages and dynamic features, alternative models can be developed to find out which difference matters and to reach robust conclusions. It is also flexible as it allows including and discarding variables easily, and above all it permits working with variables and links that are not readily measurable, even though their effects are crucial. However, its suitability to investigate SESs can be improved in several ways. The intricacy of the feedbacks can be better resolved if a specific tool for pathways analysis is developed. Returning the total number of pathways between any pair of variables and their strength can show how single pathways differently contribute to specific effects, and which of them is mostly important to mediate the effects of press perturbations. The question of link strength deserves attention. We specified in the method section that link strength is randomly assigned to the interaction link. But this does not contradict the qualitative nature of the method; it only serves to assign certainty to paths and feedbacks in order to get unambiguous predictions, which remain qualitative in nature as only the direction of change for the variables is the output. Pathway anatomy would better serve the purpose of selecting causal chain that mostly affect system dynamics. Other relevant features that would improve suitability of loop analysis include: (1) considering multiple and simultaneous press perturbations; (2) delimiting upper and lower limits for randomly assigning the strength of interactions during simulations. SESs are often exposed to different types of disturbance whose interplay gives rise to net cumulative responses that would be useful to disentangle causative chains, an important contribution to the construction of a diagnostic approach (Kittinger et al., 2013). For example, loop analysis diagnosed that multiple press perturbations and not only overfishing were responsible for the restructuring of the Black Sea community during the period 1960-1980 (Bodini et al., 2018). Moreover, socioeconomic drivers amplify the impacts that are triggered by natural processes: for instance, both hypoxia and fisheries management affected abalone stock in the Baja California SES (Martone et al., 2017). The second development might extend loop analysis towards a semi-quantitative direction. At present the simulations are performed by randomly sampling interaction strength in the uniform interval]0, 1]. This means that each interaction has an average strength of 0.5. Therefore, it is possible to calculate the magnitude of pathways of different lengths (e.g. a two-step path has strength 0.25, obtained by multiplying the strength of two interactions: 0.5 × 0.5 = 0.25). There are however cases when some interactions are known to be either strong or weak. Because it is difficult to translate strong and weak in numbers sensitivity analysis can help. Either the upper (i.e. 1) or the lower (i.e. 0, excluded) limit of interaction strength could be iteratively changed to quantify the results' consistency in the table of predictions. For example, performing the sensitivity analysis for the strength of specific interactions might help modelling competitive advantage (e.g. *Noctiluca scintillans* vs. zooplankton in the Black Sea; Bodini et al., 2018) in the ecological domain and power or information asymmetries between socioeconomic actors (Bousquet et al., 2015). Therefore, exploring alternative scenarios by constraining the strength of some interactions would be of great benefit for modelling SESs.

6. Discussion and Conclusion

Central aim of this thesis was the improvement of the *in-silica* algorithms available for loop analysis to give users a simple methodology and comprehensive tool for application of loop analysis in their protocols. Although a package as not yet been made available in the *Rs'* repository library, CRAN (R Core Team, 2019b, 2019a), a stable version of the package already exists for use, even though its dissemination is confined to participants to seminar, presentations or workshops made by us, the developers, to raise awareness of its applications and potential. As stated in ***Chapter 3***, new implementations of analytical functions are in the course of completion for future versions of the package to provide a wither range of tools for the qualitative analysis of complex systems and further functions. It is expected to have these implementations running within the package and shortly made it available, through CRAN (R Core Team, 2019a), for a wider audience of potential practitioners.

A second objective was the development, within our package, of a facility that allowed exploiting the information about the strength of interactions, to render the loop analysis algorithm more powerful in terms of its capability to explore the importance of the systems variables (and pathways) in spreading the effects of press perturbations. By exploiting and extending a background quantitative approach, used originally to solve the problem of predictions uncertainty due to the existence of multiple pathways of opposite sign, the package now allows the users to represent their ecosystems with a higher level of realism, by assigning values of intensity to the linkages between variables, and by proxy, simulating the effect of the intensity of the interactions between the variables, and how that reflects on the system's ability to respond to pressures. Derived from this implementation, another one was developed for the exploration of networks pathways and their significance, by allowing the user to gather the information of the pathways of either all or of particular sections of its network, that is, the variables involved in the pathway and therefore its length, its sign and its carried strength (i.e., the strength by which it will carry an effect from the initial variable to the last one of the path).

As demonstrated in the ***Chapters 3*** and ***4***, the new implementations developed for the *LevinsAnalysis* package have a great potential in helping resolve and understand the mechanisms behind a systems response to changes in its variables. But has proven in ***Chapter 4*** the implementation of these tools does not directly correlates to a complete understanding of the systems mechanics. In fact, from the ***Chapter 4*** it becomes clear that an in-depth knowledge of the system in study is necessary for a full and precise application of these tools, and even then, the growth of a systems complexity will only serve to raise the complexity in disentangling the information provided by these implementations. A comparison between the application of these tools in two different systems, such has the *Savannah Fires* (Bodini & Clerici, 2016) and the Caspian Sea models, from ***Chapters 3*** and ***4***, respectively, is sufficient to understand the difference that a systems complexity can have in the resolution obtained from the application of these novel approaches. While in the former we were able to find a solution to the question posed, even if a simple term, for the later, although some answers could be resolved we were also left with many more questions about the system and its complexity, questions which can only be solved with a more in-depth study and testing of the information obtained.

On ***Chapter 4***, I explored the Caspian Sea and its dynamics, with focus on the causes that lead to the decline in multiple species, in particular the kilkas (*Clupeonella spp.*). As stated throughout this body of work, the structure of the system of interest was constructed with a certain degree of realism, compatible with the evidence provided by the bulk of the literature that described the structure of that community. The possibility to use signed digraphs strictly depends on the reliability of long-term data for the abundance trend of the variables that make the network. These represent a fundamental benchmark against which model predictions can be compared. From this comparison exercise the reliability of the signed digraph as a realistic representation of the structure of the interactions should come out. Also, knowledge of the pressures acting on the system, either globally or in specific target variables, that are known to have caused specific changes or are hypothesized to have done so, must also be compiled in order to identify the entry points on the system and effects to be analysed. In short, model validation is a complex process, which requires great assimilation of facts, ecological understanding and coherent indication from the literature as well as well-structured and complete data sets.

The Caspian Sea was selected as benchmark for two reasons, 1) the small body of work dedicated to the exploration of the mechanisms behind the changes observed in that ecosystem, and 2) the rapid decline of the state of the Caspian Sea environment which calls for a rapid action based on a complete understanding of its consequences. Also, the Caspian Sea represented an interesting case study because it showed an explosion of the population of the comb jelly *Mnemiopsis leidyi* which was already observed in several of the European seas (Black Sea, Mediterranean Sea, Baltic Sea) (Javidpour, Sommer, & Shiganova, 2006; Kideys & Niermann, 1993; Vinogradov, Shushkina, Musaeva, & Sorokin, 1989). So, this study may represent another “brick in the wall” to the knowledge of the dynamics that characterize *Mnemiopsis* outburst in European seas. In the particular case of the Caspian, the outburst of *Mnemiopsis* was not investigated, as the objective was to provide a baseline knowledge of the ecological mechanisms that could be exploited to investigate the interference by the comb jelly. There is a lack of information about the species that inhabit the Caspian Sea, their relationships, and most importantly, variation in the abundance of these species in the course of time (CEP, 2002, 2007). The acquisition of the necessary data was made difficult by the lack of data pertaining the particular populations of certain species that inhabit the Caspian, with their habits and inter-species relationships being often drawn from other populations of the same species inhabiting similar seas. The geography of the Caspian Sea and the geopolitical situation of the bordering countries (Zimnitskaya & von Geldern, 2011) also conspired to make the difficulty in data access, with data reports and publications being made in a language inaccessible for me, or data on some species not even being available to public consultation. Despite these problems, an analysis was possible and from there some information regarding the system and its mechanisms of response to pressures were retrieved.

From the study presented here kilkas emerges as an important component of the system as it plays a role in the spreading of the effects of external perturbations. It comes then that any pressure on kilkas has the potential to disturb the system and make it move away from the from his state of equilibrium. Also, bony fish seem to occupy a central position in this respect. Such a pressure, as overfishing, on these variables as therefore the potential to not only cause the decline on them, as observed on the collected trends, but also to disturb other species through indirect pathways. From the hypothetical scenarios that were simulated also phytoplankton too seems to play an important role on the systems response to pressures, in particular a negative pressure on this variable produces one of the best rate of prediction and trends match, which points to its importance, and an hypothesis can be made that the water level instability in the early years of dam construction in the Volga might be the possible explanation for this negative input on phytoplankton, and therefore a further review of the literature should be made in order to verify it. Nutrients, and in particular nutrient enrichment, on the other hand seemed to not be so important in the systems response to perturbations as predictions from positive inputs on this node tended to be of opposite sign of the trends that we collected. As stated above, the interaction strength between variables may have different degrees of importance in a systems response to perturbation. In the case of the Caspian Sea, the high number of mismatches between predictions and trends, and the for some cases the prevalence of *0** signs in the predictions seems to indicate that the paths connecting the multiple variables of the system and their strength, and from there, the interactions strength between variables, seems to be of a high importance. And last, from the lack of agreement of the predictions from concurrent inputs and the trends, it can be hypothesised that either the pressures did not all occurred at the same time, even if their effect on each species might have, or their intensity was not the same, with some proving to overpower the others.

The major aim of this chapter was to build a reliable graph of the Caspian Sea network to explore the mechanisms behind the changes observed in the second part of the last century, but due to the complexity of the system and the apparent importance that interaction strength plays in the systems response to pressures, it was impossible to give a conclusive answer to the questions posed for this chapter, instead we are left with more questions, in particular to the role interaction strength and paths strength play in the Caspian Sea, and therefore a clear-cut answer on how a given pressure on the system will affect it cannot be provided without a complete understanding of how the system dynamics operate.

On ***Chapter 5*** an exercise on the potential uses of the qualitative algorithm of loop analysis beyond the ecological field is made, in particular to the possible advantages of its use on socio-ecological settings. It is shown that the method of loop analysis can be helpful. Its adaptability allows it to be used in changing contexts, such has when in doubt about critical linkages and dynamic features arises, and alternative models are necessary to be developed to reach robust conclusions. Nonetheless, its suitability to investigate SESs can be improved in several ways. The intricacy of the feedbacks can be better resolved with the use of pathways analysis. Returning the total number of pathways between any pair of variables and their strength can show how single pathways differently contribute to specific effects, and which of them is mostly important to mediate the effects of press perturbations. Considering multiple and simultaneous press perturbations and delimiting upper and lower limits for randomly assigning the strength of interactions during simulations are also implementations that would improve loop analysis suitability.

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Sezioni

Dottorati di ricerca

Il tuo indirizzo e-mail

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Oggetto:

Dichiarazione di conformità della tesi di Dottorato

Io sottoscritto Dott. (Cognome e Nome)

da Silva Pereira, Daniel Filipe

Nato a:

Vila das Aves

Provincia:

Portogallo

Il giorno:

22/05/1989

Avendo frequentato il Dottorato di Ricerca in:

Biologia Evoluzionistica ed Ecologia

Ciclo di Dottorato

32

Titolo della tesi:

Qualitative modelling of ecological systems: Extending calculation procedures and applications

Titolo della tesi (traduzione):

Modelli qualitative di sistemi ecologici: estensione degli algoritmi di calcolo e applicazioni

Tutore: Prof. (Cognome e Nome)

Bodini, Antonio

Settore Scientifico Disciplinare (S.S.D.)

BIO/07

Parole chiave della tesi (max 10):

loop analysis, qualitative modelling, r environment, complex systems, jacobian matrix, graph analysis, caspian sea, socio-ecological analysis, ecological networks

Consapevole, dichiara

CONSAPEVOLE: (1) del fatto che in caso di dichiarazioni mendaci, oltre alle sanzioni previste dal codice penale e dalle Leggi speciali per l'ipotesi di falsità in atti ed uso di atti falsi, decade fin dall'inizio e senza necessità di alcuna formalità dai benefici conseguenti al provvedimento emanato sulla base di tali dichiarazioni; (2) dell'obbligo per l'Università di provvedere al deposito di legge delle tesi di dottorato al fine di assicurarne la conservazione e la consultabilità da parte di terzi; (3) della procedura adottata dall'Università di Ferrara ove si richiede che la tesi sia consegnata dal dottorando in 2 copie di cui una in formato cartaceo e una in formato pdf non modificabile su idonei supporti (CD-ROM, DVD) secondo le istruzioni pubblicate sul sito: http://www.unife.it/studenti/dottorato alla voce ESAME FINALE – disposizioni e modulistica; (4) del fatto che l'Università, sulla base dei dati forniti, archivierà e renderà consultabile in rete il testo completo della tesi di dottorato di cui alla presente dichiarazione attraverso l'Archivio istituzionale ad accesso aperto "EPRINTS.unife.it" oltre che attraverso i Cataloghi delle Biblioteche Nazionali Centrali di Roma e Firenze; DICHIARO SOTTO LA MIA RESPONSABILITA': (1) che la copia della tesi depositata presso l'Università di Ferrara in formato cartaceo è del tutto identica a quella presentata in formato elettronico (CD-ROM, DVD), a quelle da inviare ai Commissari di esame finale e alla copia che produrrò in seduta d'esame finale. Di conseguenza va esclusa qualsiasi responsabilità dell'Ateneo stesso per quanto riguarda eventuali errori, imprecisioni o omissioni nei contenuti della tesi; (2) di prendere atto che la tesi in formato cartaceo è l'unica alla quale farà riferimento l'Università per rilasciare, a mia richiesta, la dichiarazione di conformità di eventuali copie; (3) che il contenuto e l'organizzazione della tesi è opera originale da me realizzata e non compromette in alcun modo i diritti di terzi, ivi compresi quelli relativi alla sicurezza dei dati personali; che pertanto l'Università è in ogni caso esente da responsabilità di qualsivoglia natura civile, amministrativa o penale e sarà da me tenuta indenne da qualsiasi richiesta o rivendicazione da parte di terzi; (4) che la tesi di dottorato non è il risultato di attività rientranti nella normativa sulla proprietà industriale, non è stata prodotta nell'ambito di progetti finanziati da soggetti pubblici o privati con vincoli alla divulgazione dei risultati, non è oggetto di eventuali registrazioni di tipo brevettale o di tutela. PER
ACCETTAZIONE DI QUANTO SOPRA RIPORTATO

Firma del dottorando

Ferrara, li _25/03/2020________________________ (data) Firma del Dottorando Daniel Pereira

Firma del Tutore

Visto: Il Tutore Si approva Firma del Tutore Antonio Bodini