

Identifying potential consequences of natural perturbations and management decisions on a coastal fishery social-ecological system using qualitative loop analysis

Author(s): Rebecca G. Martone, Antonio Bodini and Fiorenza Micheli

Source: *Ecology and Society*, Vol. 22, No. 1 (Mar 2017)

Published by: Resilience Alliance Inc.

Stable URL: <http://www.jstor.org/stable/26270077>

Accessed: 05-06-2018 22:40 UTC

## REFERENCES

Linked references are available on JSTOR for this article:

[http://www.jstor.org/stable/26270077?seq=1&cid=pdf-reference#references\\_tab\\_contents](http://www.jstor.org/stable/26270077?seq=1&cid=pdf-reference#references_tab_contents)

You may need to log in to JSTOR to access the linked references.

---

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://about.jstor.org/terms>



This article is licensed under a Attribution-NonCommercial 4.0 International. To view a copy of this license, visit <https://creativecommons.org/licenses/by-nc/4.0/>.



JSTOR

*Resilience Alliance Inc.* is collaborating with JSTOR to digitize, preserve and extend access to *Ecology and Society*

Research

# Identifying potential consequences of natural perturbations and management decisions on a coastal fishery social-ecological system using qualitative loop analysis

Rebecca G. Martone<sup>1</sup>, Antonio Bodini<sup>2</sup> and Fiorenza Micheli<sup>3</sup>

**ABSTRACT.** Managing for sustainable development and resource extraction requires an understanding of the feedbacks between ecosystems and humans. These feedbacks are part of complex social-ecological systems (SES), in which resources, actors, and governance systems interact to produce outcomes across these component parts. Qualitative modeling approaches offer ways to assess complex SES dynamics. Loop analysis in particular is 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. Using a case study of multispecies, multifleet coastal small-scale fisheries, we demonstrate the application of loop analysis to provide predictions regarding SES responses to perturbations and management actions. Specifically, we examine the potential ecological and socioeconomic consequences to coastal fisheries of different governance interventions (e.g., territorial user rights, fisheries closures, market-based incentives, ecotourism subsidies) and environmental changes. Our results indicate that complex feedbacks among biophysical and socioeconomic components can result in counterintuitive and unexpected outcomes. For example, creating new jobs through ecotourism or subsidies might have mixed effects on members of fishing cooperatives vs. nonmembers, highlighting equity issues. Market-based interventions, such as ecolabels, are expected to have overall positive economic effects, assuming a direct effect of ecolabels on market-prices, and a lack of negative biological impacts under most model structures. Our results highlight that integrating ecological and social variables in a unique unit of management can reveal important potential trade-offs between desirable ecological and social outcomes, highlight which user groups might be more vulnerable to external shocks, and identify which interventions should be further tested to identify potential win-win outcomes across the triple-bottom line of the sustainable development paradigm.

**Key Words:** *ecosystem-based management; loop analysis; small-scale fisheries; social-ecological systems; trade-offs*

## INTRODUCTION

Mounting evidence of ecosystem degradation and the resulting reciprocal effects on human well-being have led to calls for comprehensive ecosystem-based management worldwide. Natural resource management has moved away from approaches that focus on a single species or sector, view the environment as static, and separate social and ecological issues toward integrated, dynamic approaches that consider the entire ecosystem, including humans, interactions among social and ecological components, and the cumulative impacts of multiple activities (Hughes et al. 2005, McLeod et al. 2005, Leslie and McLeod 2007, Levin et al. 2009). This shift reflects the view that managing for sustainable development and resource extraction requires an understanding of the feedbacks between biophysical systems and humans, and thus requires an integrative, interdisciplinary approach. These feedbacks are part of social-ecological systems (SES), in which resources, actors, and governance systems interact to produce outcomes across these component parts (Berkes and Folke 1998, Ostrom 2009, Cox et al. 2010, McGinnis and Ostrom 2014).

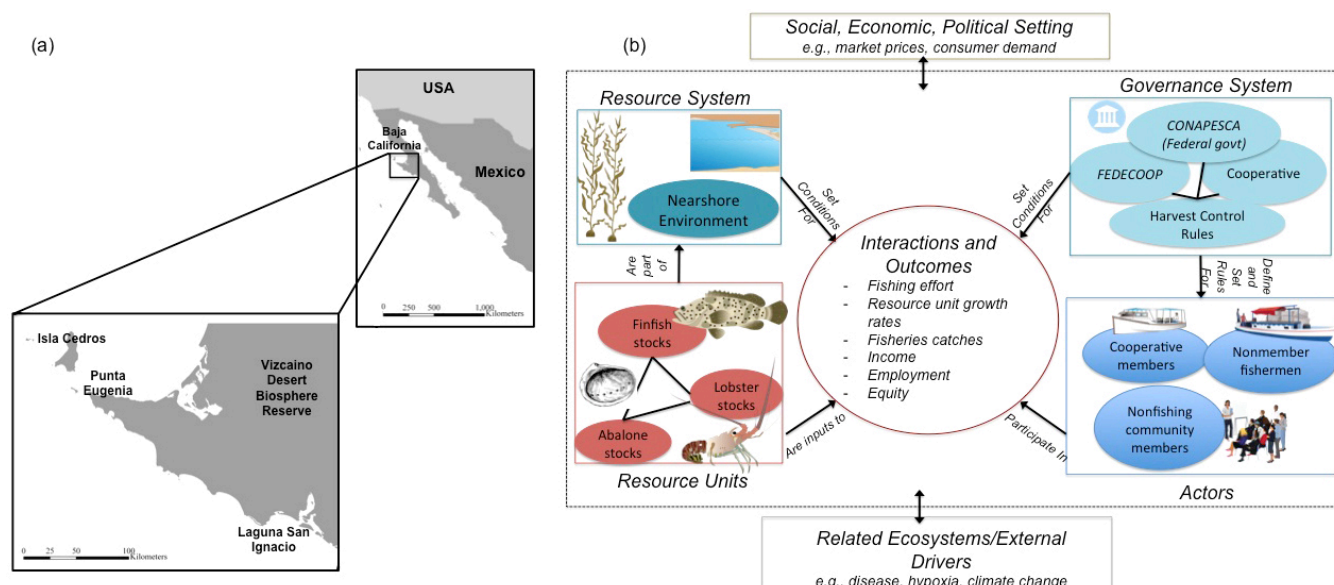
Marine ecosystems and the fisheries they support are examples of complex SES, with numerous relationships among ecological, social, economic, and institutional components operating at multiple scales (Berkes 2006, Mahon et al. 2008, Levin et al. 2009, Berkes 2011, Halpern et al. 2012, Kittinger et al. 2013). Governance and financial systems interact with social systems to influence human behaviors, which in turn have an impact on the marine and coastal environments, while the marine environment

and resource units can in turn influence the choice of operational and collective-choice rules, and economic and cultural values (Fig. 1). All of these elements interact to produce a set of dynamic outcomes (Berkes and Folke 1998, Mahon et al. 2008, Ostrom 2009, McGinnis and Ostrom 2014). Current marine resource management recognizes the importance of considering interactions among fisheries components to meet social, ecological, and economic sustainability, but it can be challenging to develop an explicit understanding of the direct and indirect effects of fisheries on the larger web of interacting species and the feedbacks among these components on the greater social-ecological network. The processes to be quantified and modeled are numerous and produce feedbacks whose effects are difficult to predict. These complex dynamics often exceed our current understanding and data availability. However, to inform decision making and guide future monitoring and management actions, managers must evaluate the consequences of management actions or of external perturbations to the system (e.g., drivers associated with climate change, market fluctuations) on the full SES to avoid unintended consequences and to adaptively manage.

A suite of modeling frameworks have been developed to examine biological and human responses to multiple external and internal drivers within coupled SES (MIMES, Boumans and Costanza 2007; InVEST, Nelson et al. 2009; Atlantis, Fulton et al. 2011). Most of these models require large amounts of data because system components are numerous and feedbacks are complex. An alternative to an in-depth, quantitative description of SES and

<sup>1</sup>Center for Ocean Solutions, Stanford University, <sup>2</sup>Department of Life Sciences, University of Parma, Italy, <sup>3</sup>Hopkins Marine Station, Stanford University

**Fig. 1.** The fishing cooperatives of the Vizcaino region in Baja California Sur, Mexico: (a) map of the study area showing location along the coastline from Punta Eugenia to Laguna San Ignacio; (b) conceptual representation of the social-ecological system (SES) based on the updated SES framework presented in McGinnis and Ostrom (2014).



their dynamics is qualitative modeling. Qualitative modeling approaches, including fuzzy cognitive mapping (Kok 2009), causal loop diagrams (Lane 2008), Bayesian belief networks (Woolridge and Done 2004), and loop analysis (Puccia and Levins 1986), can provide practical tools for evaluating external perturbations and management strategies, particularly under circumstances of limited data availability and uncertainty in the nature and strength of relationships within and between socioeconomic and biophysical components (Fishwick and Luker 1991, Dambacher et al. 2007, Espinoza-Tenorio et al. 2013, Carey et al. 2014). Furthermore, they can be developed using participatory approaches with multiple stakeholders and have conceptual appeal, are intuitive, and represent good communication tools. Loop analysis is one particular technique that allows for investigations of the dynamics of complex systems when the signs of interactions are known but other aspects of the linkages are uncertain, including strength of the interactions and their functional forms and parameters; in other words, whether a system component (e.g., species, actors, or user groups) has a positive, negative, or no effect on another component with which it interacts. Despite its limitations (see discussion of merits and limitations in Justus 2006), the limited data requirements of loop analysis make it a promising tool for investigating the dynamics of SES in data poor systems.

Loop analysis allows for an examination of how an external press perturbation (Bender et al. 1984) would potentially spread its effects in a system across multiple socioeconomic and ecological variables through the network of interactions among the variables. In loop analysis, linkages between variables are representations of the directional effect that one variable has on the rate of change of the other. For example, for predator-prey relationships, an increase in a predator population leads to a decrease in the growth rate of its prey. These linkages are expressed

mathematically by the coefficients of the Jacobian matrix of a system of differential equations. The sign of these coefficients identify how any one variable qualitatively affects the others. By following the direction of links one can reconstruct the pathways of interactions through which management actions or natural perturbations propagate beyond the target variable. The abundance or level of any of the variables in the system may be predicted to increase, decrease, or remain the same following the natural perturbation or management intervention.

Thus, loop analysis offers alternatives to quantitative modeling for dealing with the complexities of SES in data poor systems and provides testable hypotheses regarding SES responses to perturbations and/or management actions (e.g., Carey et al. 2014). Although loop analysis offers an analytical framework for investigating the complexity of marine social-ecological systems (Espinoza-Tenorio et al. 2013, Carey et al. 2014, Reum et al. 2015), many applications of this approach to date have focused on the ecological elements of the system and have not included aspects of the social system and key SES linkages (but see Dambacher et al. 2007).

We apply qualitative loop models to examine changes in coastal SES of the Vizcaino Peninsula, Baja California, Mexico, in response to natural perturbations and management actions that have recently been implemented or are currently under consideration. These coastal fisheries are particularly relevant as a model system because fishing cooperatives of this region were granted exclusive access rights to a suite of invertebrate species starting in the 1930s (McCay et al. 2014), whereas fishing for finfish or by fishermen that do not belong to cooperatives has remained open access. Thus, this system allows for an examination of the ecological and socioeconomic consequences of allocating access rights for different species and to different users (e.g.,

Pomeroy et al. 2001, Costello et al. 2008), a management approach that is currently being implemented in small-scale fisheries globally (<http://www.bloomberg.org/program/environment/vibrant-oceans/>).

Using a case study of multispecies, multifleet, coastal, small-scale fisheries, we demonstrate the application of loop analysis to examine interactions among ecological and socioeconomic variables associated with territorial user right fisheries (TURF)-managed commercial fisheries and to understand the main feedbacks that drive the social and ecological performance of these coupled systems. We demonstrate how loop analysis can be applied as a method for examining potential outcomes from scenario analysis to inform planning and monitoring in SES. Through this approach, we examined a set of scenarios that mimic perturbations to the SES including the effects of climate perturbations that have recently been associated with observed decline in different stocks (e.g., Micheli et al. 2012), market-based initiatives such as an ecolabel, which was awarded to one of the fisheries (the spiny lobster trap fishery) operating in this region (Micheli et al. 2014a), and of changes in fisheries management and governance that are currently under consideration (Micheli et al. 2014b). Although these scenarios are designed to capture perturbations and management actions specific to the Vizcaino fisheries, they represent impacts faced by many coastal fishing communities worldwide and management options available to several of these communities. Because the application of loop analysis is relatively novel in the field of fisheries management (but see Espinoza-Tenorio et al. 2013, Carey et al. 2014), we emphasize, through the analysis of realistic scenarios in a case study system, the potential of loop analysis to evaluate complex social-ecological systems. Our analysis should provide useful insights for a suite of small-scale fisheries, in addition to the Vizcaino region cooperatives, to identify hypotheses and key variables for monitoring. Specifically, we ask: (1) What are the anticipated biological and socioeconomic consequences of external perturbations that result in the decline of specific stocks? (2) What market-based, governance, or local management actions may result in both biological and socioeconomic benefits? Which of these actions may result in resource declines or negative socioeconomic impacts? (3) How does the representation of the system (i.e., what specific linkages and feedbacks among system components are included) influence the predicted responses to perturbations?

## METHODS

### Study system/conceptual model

To illustrate and describe the components, linkages, interactions, and potential outcomes of the Vizcaino fisheries system, we developed a conceptual model based on Ostrom's social-ecological system (SES) framework (Ostrom 2009, McGinnis and Ostrom 2014), available literature describing the system, and the authors' knowledge of the system (Martone 2009, Shester and Micheli 2011, Micheli et al. 2012, 2014b, McCay et al. 2014; Fig. 1). Components are organized as resource units, which interact among themselves and are part of a larger resource system that is subject to external forces that can influence the system, such as market or other socioeconomic drivers and global environmental change. The governance system defines a set of rules for a set of actors, some of whom are resource users. These systems and their

components then interact in different ways to produce social and ecological outcomes. Finally, we indicate related drivers and conditions that are external to the system but which influence the components and their interactions.

### Resource System

The study cooperatives are located along the Vizcaino Peninsula of the Pacific coast of central Baja California, Mexico, a region known as the Pacifico Norte (Fig. 1). The Pacifico Norte region can be characterized as temperate to subtropical, with sea surface temperatures ranging from 12–27 °C throughout the year. The region is a mosaic of rocky reef and sandy subtidal ecosystems that encompass the southern edge of the range of giant kelp (*Macrocystis pyrifera*) in which a zone of persistent upwelling maintains high biological productivity (Martone 2009).

### Governance

The cooperatives belong to the Federacion Regional de Sociedades Cooperativas de la Industria Pesquera de Baja California (FEDECOOP), which acts as a comanagement agency with the national and regional fisheries agencies to monitor resources and develop management plans. The fishing cooperatives of the Pacifico Norte date back to the late 1930s, as a manifestation of the Mexican cooperative movement that was mainstreamed into national fisheries development policies (Ponce-Díaz et al. 2009, McCay et al. 2014). From the beginning of the cooperatives, access to high-value fisheries, such as lobster (*Panulirus interruptus*) and abalone (*Haliotis* spp.), in adjacent fishing grounds has been restricted by law to cooperative members. Since 1992, this special right has been in the form of 20-year concessions for exclusive exploitation rights for some species, including lobster and abalone.

The long-term exclusive concessions held by the cooperatives are examples of the assignment and comanagement of community-based access, withdrawal, exclusion, and management rights (Schlager and Ostrom 1992, Pomeroy et al. 2001). These community-based access rights have enabled cooperatives to add and enforce conservative management measures, including, but not limited to, regulation of catch composition, seasonal closures, and size limits in lobster fisheries (Vega 2001), reef-specific quotas, and the voluntary establishment of no-take reserves exclusively aimed at rebuilding abalone populations and other fisheries targets (Micheli et al. 2012, McCay et al. 2014). Both cooperative and noncooperative members are compliant with rules because of both positive and negative incentives that come with membership in the cooperative and ongoing investment in monitoring, enforcement, and infrastructure (McCay et al. 2014). However, the lack of concessions and associated rights for finfish may impede management of these stocks in this region, given that the incentives that often accompany comanagement and exclusionary rights are not in place for these species (Shester and Micheli 2011, Micheli et al. 2014a).

### Resource Units

The Pacifico Norte fisheries target a wide variety of interacting species in rocky reef food webs, including predators, such as lobster and several finfish species, and their prey and competitors. Currently, in addition to lobster and abalone, cooperatives have exclusive rights to a set of other benthic species, including the wavy turban snail *Megastrea undosa*, the sea cucumber *Parastichopus parvimensis*, the red sea urchin *Mesocentrotus*



*franciscanus*, and the red alga *Gelidium robustum*. The cooperatives also catch finfish, primarily barred sand bass (*Paralabrax nebulifer*), ocean white fish (*Caulolatilus* spp.), and California halibut (*Paralichthys californicus*) using nets and traps. In contrast with benthic invertebrates and algae, cooperatives do not hold territorial rights for finfish, so fishermen that are not members of the fishing cooperatives also have access to these species.

#### Actors

The FEDECOOP fisheries are located on the coastal edge of a vast desert protected by UNESCO biosphere reserve designation since 1988 (Fig. 1). The remote nature of these fisheries in combination with their unique institutional structure and history of occupation along the coast leads to the cooperatives playing a strong role in the community. Collectively, the cooperatives provide infrastructure, social programs, and employment to many residents in the communities, including both cooperative members and nonmembers, in jobs involving harvest, rule enforcement, resource monitoring, seafood processing, and transportation (Ponce-Díaz et al. 1998; Fig. 1).

#### Socioeconomic and ecological interactions and outcomes

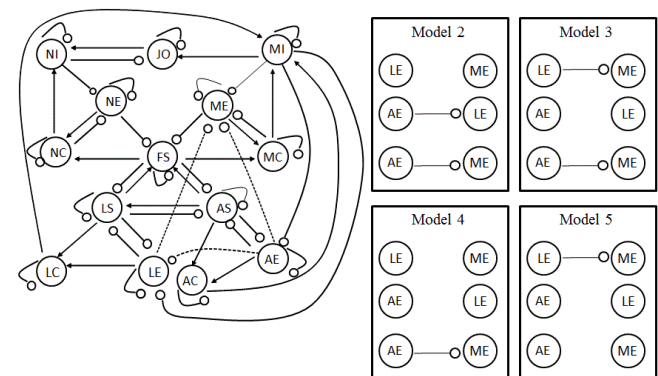
Membership in the cooperatives brings social and economic benefits. Abalone and lobster are the main targets and provide high value to the cooperatives because of high demand and market prices for these commodities (McCay et al. 2014). Finfish fisheries are also economically important in the region, representing additional, and in some cases the most important income source for cooperatives (Shester and Micheli 2011). Moreover, opportunities to engage in finfish fishing provide additional income for cooperative members during the closed fishing season for their main target species, as well as income and subsistence harvest for noncooperative members in the community, who do not have access to benthic fishery targets that are the purview of the cooperatives (Shester and Micheli 2011). However, despite delivery of important benefits to cooperative members and nonmember fishers, the gear types used by this fishery tend to have higher by-catch rates and may have adverse long-term effects on target populations, food webs, and habitats (Shester and Micheli 2011, Micheli et al. 2014a, b).

#### Loop analysis

The loop analysis first translates the conceptual model (Fig. 1) into a pictorial representation of interactions between the SES components, including resource units (e.g., species, fisheries catch), actors (e.g., cooperative members and noncooperative fishers), the governance system (e.g., harvest control rules, fishing effort), and socioeconomic factors (e.g., income, jobs for noncooperative members; Fig. 2). We assembled the SES interaction web capturing some of the main biological and socioeconomic components in our conceptual model (Fig. 1) and illustrated the linkages among them in a signed digraph (Fig. 2; Appendix 1). We represent biological linkages as possible trophic relationships among target species or species groups, the linkages among species and fisheries operating in the study region based on harvest control rules, and key actors and some relevant socioeconomic components of the system (Fig. 2). The interaction web was assembled based on authors' experience and knowledge of the system and from relationships described in the published literature, including data from sampling and taxonomic

identification of the benthic fauna and flora, stomach content analyses of fish and invertebrates, interviews with fishermen and cooperative members, and household surveys (Shester 2008, Martone 2009, Morales-Zárate et al. 2011, Ramírez-Sánchez et al. 2011, Shester and Micheli 2011, McCay et al. 2014, Leslie et al. 2015).

**Fig. 2.** Signed-digraph representation of the social-ecological system (SES) interactions in the Baja California fisheries case study. Variables are : MI (cooperative member income); JO (job opportunities for nonmembers); NI (nonmember income); ME (members effort on finfish); NE (nonmembers effort on finfish); MC (finfish catch by members); NC (finfish catch by nonmembers); FS (finfish stock); LE (lobster effort, by members only); LC (lobster catch); LS (lobster stock); AE (abalone effort, by members only); AC (abalone catch); and AS (abalone stock). Arrows represent positive interactions, where a variable leads to a positive rate of change in the other, and lines with open circles represent negative interactions, where a variable inhibits the rate of change in the other. The main model (model 1) includes predator-prey relationships among the three stocks, abalone, lobster, and finfish, and negative relationships among fishing effort between the abalone and lobster fisheries and the lobster and finfish fisheries. The other four model structures are variations on this primary model and remove some of the linkages among fishing efforts (models 2-5).



Loop analysis qualitatively predicts average changes in variables of interest (e.g., species abundance or catch) in response to varying conditions that modify their rate of change, i.e., variations in parameters governing the rate of change for the variables. One example is a stressor that increases the mortality rate of a species. This reduces that species' population growth rate, which in turn influences the abundance of that species as well as that of the other species to which the latter is connected in the network. The variation in the level of a component  $j$  due to a parameter change can be calculated by the loop formula:

$$\frac{\partial x_j}{\partial c} = \frac{\sum_{i,k} \left\{ \left[ \frac{\partial f_i}{\partial c} \right] \times \left[ p_{ji}^{(k)} \right] \times \left[ F_{n-k}^{(comp)} \right] \right\}}{F_n} \quad (1)$$

where  $c$  is the changing parameter (e.g., mortality, fecundity, predation rate);  $\partial f_i / \partial c$  designates whether the growth rate of the

$i$ -th variable is increasing, decreasing (positive or negative input, respectively);  $p_{ji}^{(k)}$  is the pathway connecting the variable that undergoes parameter change,  $i$ , with the variable whose equilibrium value is being calculated,  $j$ , and which includes  $k$  variables;  $F_{n-k}^{(comp)}$  is the complementary feedback, which buffers or reverses the effect of the pathway. The denominator indicates the overall feedback of the system, which is a measure of the inertia of the whole system to change. A more detailed explanation of the method of loop analysis and the algorithm for predictions is given in Appendix 1. Loop analysis models were run in R using a code that is provided in Appendix 2.

### Biological links

For our resource units, we included three main target species and species complexes in our loop analysis: lobster stocks, abalone stocks, and finfish stocks. We represent the following biological interactions in the social-ecological system: lobster are known predators of molluscs including abalone (Braje et al. 2009); finfish, such as gulf grouper (*Mycteroperca jordani*), cabezon (*Scorpaenichthys marmoratus*), and sheephead (*Semicossyphus pulcher*), are predators of both lobster, particularly the juvenile stages, and abalone (Braje et al. 2009; Fig. 1). Thus, abalone (AS), finfish (FS), and lobster (LS) form a tri-trophic system: FS preys upon both AS and LS, while LS preys upon AS. All stocks have negative feedback loops to themselves, representing density-dependent effects on population growth rate. Because these predators are all generalists and the degree to which these interactions drive top-down or bottom-up processes are unknown in this system, we tested the effects of including these interactions in the network in three different models, including top down and bottom up effects, bottom up effects only, and no biological interactions. This latter case explores the situation in which the biological interactions are completely obscured by socioeconomic links in determining the dynamics of fish variables.

### Fisheries links

The Pacifico Norte cooperative fisheries target lobster using traps, abalone using hookah diving, and finfish using a variety of gear types, including traps, set gillnets, and driftnets (Shester and Micheli 2011, Micheli et al. 2014b). As in most fisheries, we assume that stock and effort have positive effects on catch, catch has a negative effect on stock, and effort and stocks have negative effects on each other (Fig. 2). The negative link from stock to effort considers that the larger the stock, the lower the effort required to obtain the same catch. Factors that control the fisheries are translated in the model as a self-damping term on effort and catch, representing the action of other variables that are not included in the model but can regulate model components (Bodini 1988). Although several factors, beside the density-dependent mechanism, can generate a self-damping term on variables (Puccia and Levins 1986), we do not include this mechanism in all of our variables, because the inclusion of all variables that play a regulative effect on the system in the model would make the model intractable. Because these fisheries are all conducted under the same cooperative system by the same fishers, and abalone and lobster are the main cooperative targets, we have linked effort among fisheries, such that both lobster and abalone effort negatively affect the rate of change of finfish effort, and abalone effort is negatively linked to lobster effort. We tested the effects of including these linkages on the outcomes of the SES by varying our model structure (Fig. 2).

In addition to the linkages among fishing efforts within the cooperatives, there are also nonmembers that have access to finfish stocks because the cooperatives do not hold exclusive access privileges for finfish. We captured nonmember effort separately by linking it negatively to the same finfish stock that is targeted by the cooperatives (Fig. 2). Nonmember effort is positively linked to nonmember finfish catch and is negatively linked to finfish stock size (Fig. 2).

### Socioeconomic links

Both cooperative members and nonmembers gain income directly from the catch of stocks. Therefore, nonmember finfish catch positively affects nonmember income, whereas finfish, abalone, and lobster catch all positively affect member income (Fig. 2). In all of our models, income negatively affects effort. Furthermore, to capture the positive effect that cooperatives have on nonmembers in these communities through the provision of job opportunities (e.g., in seafood processing plants), member income positively affects job opportunities in the community and jobs positively affect nonmember income (Fig. 2).

### Predicting change through loop analysis

The loop formula (1) allows predictions of how the level of system components might change because of external forcing (Puccia and Levins 1986). Predictions calculated with the loop formula can be arranged in a table with signs showing the expected direction of change (+, -, or 0). In Figure 3, signs for predictions are substituted by arrows for a clearer presentation. The entries in the table denote variations expected in the column variables when positive parameter inputs affect each row variable. Each row of the table indicates the variable that is subjected to parameter change. The responses of the variables to variations in the rate of change of a given row variable are reported in the columns. These responses concern the direction of change of the level of the variables (e.g., biomass, number of individuals, or amount of money). Predictions are conventionally obtained for positive input. In the case of a negative input, predicted directions of change along the row of interest are simply inverted.

Model variables are often connected to each other by multiple pathways. If such pathways have opposite effects, the model can yield ambiguous predictions. In these cases, model predictions are undetermined, and + or - signs in the table of predictions are replaced by question marks (?). To address these ambiguous predictions, we used a routine that randomly assigns numerical values to coefficients of the community matrix (i.e., the coefficients of the links in the signed digraph). Values for links are generated randomly by a routine within the interval  $(10^{-6} - 1)$ . This procedure is executed  $n \times n \times 100$  times, where  $n$  is the number of variables in the model. Therefore we created for each model community matrices ( $n = 14$ ; Total runs = 19,600). Community matrices can then be inverted to understand how variables affect each other directly and through indirect pathways (Bender et al. 1984, Wootton 2002, Montoya et al. 2009). The coefficient  $(cij^{-1})$  of the inverse community matrix shows the overall effect of variable  $j$  on variable  $i$  due to its direct link to variable  $i$  (e.g., predation, catch), as well as all possible indirect pathways through which variable  $j$  is connected to  $i$  via intermediate components. Hence, the net effect (the sum of the direct and indirect effects) of a perturbation on variable  $j$  on variable  $i$  is given by the element of the inverse community matrix.

**Fig. 3.** Table illustrating expected directional changes in the levels of the components of model 1 (Fig. 2). Alteration in the rate of change of any row variable results in expected variations in the level of the column variables. Green arrows indicate a positive change (75-100% of the linkages from the model runs were positive), whereas green triangles indicate a tendency toward a positive change (60-75% of the linkages were positive). Red arrows indicate a negative change (0-25% of the linkages from the model runs were positive), while red triangles indicate a tendency toward negative change (25-40% of the linkages were positive). Zeros (yellow dots) reflect compensation between positive and negative effects that result from the model runs and likely no change would be expected in the variable's level. Predictions are obtained by assuming positive inputs (i.e., increased rates of change of the variables) to the row variables. Predictions for negative inputs (decreased rates) can be easily obtained by simply inverting the direction of the arrows and of the triangles (and the colors). The first letter of the variable labels (in the rows and columns) identifies a system component (e.g., A for abalone, L for lobster, F for finfish), the second letter a specific descriptor of that component (e.g., S for stock size, E for effort, C for catch; see Figure 2 legend for a complete list of the variables and their acronyms).

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO
AS	↑	↓	●	↓	↑	●	↑	↓	↑	↓	↑	↑	↑	●
AE	↓	↑	↑	↑	↓	↓	↓	●	↓	↑	↓	●	↓	●
AC	●	↓	↑	●	●	↓	↑	↓	●	↓	●	↑	↑	↑
LS	↓	↑	↑	↑	↓	●	↑	●	●	↓	●	↑	↑	↑
LE	↑	↓	●	↓	↑	↑	↑	↓	↓	↓	↑	●	↑	●
LC	●	↓	↓	●	↑	↑	↑	↓	↑	↓	●	↑	↑	↑
FS	●	●	●	↓	↑	↓	↑	↓	↑	↓	↑	●	↑	↓
ME	●	↓	↓	↑	↓	●	↑	↑	↑	↓	↓	↑	↑	↑
MC	●	●	●	↑	↓	↑	↑	↑	↑	↓	↑	●	↑	↓
NE	●	●	●	↑	↓	↓	↓	↑	●	↑	↑	●	↑	↓
NC	●	●	●	↓	↑	↓	↑	↓	●	↑	↑	●	↑	↓
MI	●	↓	↓	●	↑	↓	↑	↓	●	↓	●	↑	↑	↑
NI	●	●	●	↓	↑	↓	↑	↓	●	↓	↑	●	↑	↓
JO	●	●	●	↓	↑	↓	↑	↓	●	↓	↓	●	↑	↑

The community matrix  $AH$  must have a nonzero determinant and must admit an inverse matrix  $(AH)^{-1}$ . Of the  $n \times n \times 100$  matrices created for each model, only those that satisfied the Lyapunov conditions of stability were kept and inverted. An overall table of predictions for each model was then obtained from the inverted matrices. In this table, each prediction was determined on the basis of the percentage of positive, negative, or zero signs in the array of the inverted stable matrices (Appendix 1, Table S2). We defined a set of rules to translate the percentage of cases obtained from loop analysis runs into signs in the overall prediction matrix (Puccia and Levins 1986). Specifically: - indicates that 0-25% of the relationships were positive; ?- indicates 25-40% of the relationships were positive; 0\* indicates 40-60% positive change relationships; ?+ indicates 60-75% of linkages were positive; and a + indicates 75-100% of the signs obtained in the procedure were positive. This is based on Puccia's 3:1 ratio rule (Puccia and Levins 1986). Note that 0\* are not real zeros but a neutral result that occurs when matrices have large numbers of opposite signs for a given variable's response. In fact, when multiple pathways have opposite effects to the same variable, positive and negative effects tend to compensate each other and the net result may be zero (no variation) or, more likely, a small change, which can be reasonably considered negligible.

#### Model structure and scenario testing

We examined the system dynamics and behaviors by conducting two different types of analyses. First, we explored the effects of different assumptions about model structure, particularly which linkages between variables are included or excluded (five model structures). Second, we investigated the system responses to perturbations (considering seven different perturbation scenarios).

To examine the sensitivity of model results to the specific linkages included, we varied model structure by including or removing different sets of biological and/or fisheries linkages. Models 1-5 (Fig. 2; Appendix 1, Table S2) include all of the biological linkages, in which both effects of predator and prey are represented, but each model varies the relationships among fishing effort, including or removing hypothesized links between abalone and lobster fisheries, lobster and finfish fisheries, and abalone and finfish fisheries.

We also varied the core biological structure to examine the robustness of outcomes to different assumptions about how species may affect each other through consumer-resource interactions. In a second set of models, we removed all biological linkages and varied the relationships among fishing efforts, as described above for models 1-5. In a third set of models, we included biological links but only in the form of the beneficial effect that prey exerts upon its predator, i.e., a bottom-up effect of resources on consumers. In all of these cases, the models yielded a zero matrix determinant and no predictions could be obtained. This means that the full set of biological interactions is needed for models to generate meaningful predictions. Thus, we present and discuss results only for models 1-5 (Fig. 3; Appendix 1, Table S2).

We investigated responses of single variables to parameter changes in the system by examining: (a) the table of predictions for each model to explore what relationships emerge between the ecological and socioeconomic components, and within the three fisheries; and (b) seven scenarios associated with specific external perturbations and management actions to examine the response of variables of interest, both biological (stock abundance) and socioeconomic (jobs, income).



### *Environmental perturbations*

Disease, hypoxia, and climate change are major drivers of change in marine ecosystems and are associated with increased mortality of fisheries species in many coastal fisheries (Defeo and Castilla 2012, Micheli et al. 2012). In scenario 1, we simulated the external forcing of climate or other human impacts through decreased growth rate of abalone. Hypoxia, frequent or extreme El Niño–Southern Oscillation (ENSO) events, disease, or harmful algal blooms underlie observed abalone declines and may lead to further decline by increasing abalone mortality (Morales-Bojórquez et al. 2008, Micheli et al. 2012). In scenario 2, we modeled effects of disease or ocean acidification impacts on lobster populations as a negative input to lobster stocks, reflecting an increase in lobster mortality or a decrease in lobster growth and reproduction from these external drivers. Studies of the effects of ocean acidification on crustaceans indicate likely negative impacts on growth due to rises in  $[H^+]$  in haemolymph and reduced oxygen delivery to the tissues (see Whiteley 2011 for review). Although disease has not affected lobster stocks in this system, it is a major concern for other lobster fisheries (e.g., Steneck et al. 2011).

### *Socioeconomic drivers*

We examined the effects of market-based initiatives, such as the existing Marine Stewardship Council (MSC) ecolabel or proposed system-wide certification schemes that are implemented with the goal of increasing income to the fishing cooperatives (Micheli et al. 2014a). We modeled these drivers in scenario 3 as positive inputs to the cooperative member income, although in the case of the Vizcaino cooperatives, although the eco-label allows for some increased access to higher prices in the US market, it primarily functions as a source of empowerment and helps the cooperatives maintain their concessions (Pérez-Ramírez et al. 2012a, b). Other initiatives have been proposed for this region with the aim of increasing job opportunities for noncooperative members, such as abalone pearl culture and ecotourism. In scenario 4, we tested the effects of change to nonmember income through these opportunities accessible to nonmembers of cooperatives, designed to provide alternatives to fishing.

### *Fisheries management actions*

Though not yet implemented, decreasing finfishing effort and phasing out of set gillnets has been highlighted as a possible option for decreasing the environmental impacts and improving the long-term sustainability of these cooperative fisheries (Peckham et al. 2007, Shester and Micheli 2011, Micheli et al. 2014b). In scenario 5, we examined how these management actions would influence other variables in the system using a negative input to cooperative member finfish effort. In scenario 6, we examined the effects of controls on nonmember finfish effort on the system. Finally, in scenario 7, we examined the effects of increased job opportunities through subsidies provided by the government, private foundations, or NGOs.

### **Sensitivity analysis**

To examine whether model structure affected outcomes, we compared the tables of predictions from the five models to see whether there was concordance among them. We compared each prediction matrix, for each model, to all other matrices in a series of pairwise comparisons and determined the number of cases in which each prediction matrix differed from all others (Appendix 1, Table S3).

## **RESULTS**

### **Model predictions: social-ecological systems (SES) dynamics**

Loop analysis reveals that changes in input variables (e.g., stocks' growth rates, rate of change in member income) may influence other variables in the system in directions that often cannot be predicted based on known (or assumed) directional relationships. For example (see Fig. 3), an increase in the abalone growth rates (positive input to AS) is predicted to reduce lobster stock, which is counter to the notion that prey species should positively influence the abundance of their predators. This is because the influence of a variable on any other is mediated by the other variables in the system through indirect effects.

Another surprising outcome is changes in predators leading to no effects on their prey. The correlations between predators and prey vary depending on which stock is perturbed, because of feedbacks and compensation throughout the SES. For example, when the finfish stock's (FS) growth rate increases, FS itself is predicted to increase, but abalone stock (AS) does not change (Fig. 3). This result could be interpreted as a result of FS preying upon AS but also on LS, which, in turn preys upon AS. So the effect of FS on AS is at the same time positive and negative because this species also feeds on a predator of AS. However, the complexity of the SES increases the multiplicity of the pathways that connect FS and AS. The loop analysis indicates that FS is connected to AS by eight paths: four paths with a negative sign and four positive (the product of the signs of the links yield the overall sign for the path; see Appendix 1, Table S1). Thus, our simulations yielded the same percentage of matrices in which AS is expected to increase and matrices in which AS is expected to decrease (50%), resulting in a compensation of effects and a magnitude of variation that can be close to zero.

A positive input on FS causes lobster stock (LS) to decrease. This negative effect that LS experiences when a positive input affects the growth rate of FS could be due to the direct predation on LS and the predation on its prey. However, in a complex system like the one we describe in Figure 2, any effect of one variable on another is mediated by multiple pathways, so the full set of pathways must be examined to understand the effects.

Nine pathways connect FS to LS (Fig. 2; Appendix 1, Table S1). Five carry a negative effect to LS and four carry a positive effect. Although there is only one additional path indicating negative effects of FS on LS, the numerical simulation yielded that only 8% of the matrices predict an increase for the level of LS with a positive input affecting FS. But 91% of the matrices predict the population of LS to decrease following a positive input to FS. This is surprising, given that with the quasi-balanced number of pathways carrying opposite effects, we would expect the results of the simulation be more equilibrated. Likely this discrepancy between what we would expect looking at the number of pathways and what we obtain from the simulations depends on the following: random coefficients are taken in the range  $10^{-6}$ –1, but the product of link values in longer paths yields smaller numbers than the shorter paths; so that these latter contribute more to the final outcome from the loop analysis. If we consider the pathways from FS to LS (Appendix 1, Table S1), the two shortest pathways both have negative signs and we can understand why despite the numerical quasi-balance between opposite pathways, the response of LS to an increase in the growth rate of FS is negative.



In the previous case (input to FS and effect on AS), instead, the two shorter paths (Appendix 1, Table S1) have opposite signs. This relationship between FS and LS is consistent with what is anticipated from known predator-prey relationships, with some of the finfish species targeted by local fisheries (e.g., sheephead, *S. pulcher*) preying on lobster (i.e., an anticipated negative effect of increased FS on LS).

Despite expected negative effects on AS from FS and LS as predators, a positive correlation emerges between AS and FS when there is a perturbation to AS, whereas either no correlation or a negative correlation is predicted between AS and LS. As inputs enter the system through lobster stock (LS), LS becomes negatively correlated with AS, whereas no correlation exists between these two variables and FS, the abundance of which in all five models is predicted not to change.

The table of predictions can be used as a diagnostic tool to detect the entry point(s) of perturbations. For example, abalone stock (AS) changes only if perturbations enter the system through the abalone and lobster fisheries in the form of input to stocks and effort for both these fisheries. The only exception is model 4 (Appendix 1, Table S2), in which input to effort on finfish by members of the cooperative (ME) is predicted to affect abalone stock. According to these results, any variation in AS can be associated to alterations in the abalone or lobster fisheries but not in other variables of the system (i.e., economic variables).

Examining relationships between the fishery variables (catch, effort, and stocks) can also provide insights in the dynamics of specific fisheries. For example, the 3 x 3 submatrix that includes the relationships among variables AS, AE, and AC (abalone stock, fishing effort, and catch; Fig. 3) can be examined to glean information about aspects of the abalone fishery. As expected, abalone stocks are negatively correlated with effort: as effort increases, stock decreases and vice-versa. Effort and catch are positively correlated in one direction but negatively correlated in the other direction: as effort increases, catch increases, but as catch increases, effort is predicted to decrease. However, stock and catch show a neutral relationship, suggesting that effort is the key control variable. This submatrix is identical across all five models that we investigated (Appendix 1, Table S2), suggesting that conclusions based on this submatrix are robust to variations in model structure.

The table of predictions can also indicate which variables are most susceptible to external perturbation, either from environmental change or management interventions. For example, member income (MI) shows a greater inertia than nonmember income (NI) to parameter changes (Fig. 3). In model 1, 8 out of 14 possible responses of MI to external inputs are null (Fig. 3), and this pattern changes only slightly in the other models (the number of zeros varies between 6 and 8; Appendix 1, Table S2). Nonmember income remains unaltered only when inputs enter the system through AE, LS, and ME, in various combinations for the five models. Thus cooperative member income seems less vulnerable to perturbations than nonmember income, but it is also predicted to be less responsive to management interventions.

## Predicted outcomes of natural perturbations and management actions

### *Collapse of target taxa (scenarios 1 and 2)*

Disease and climate change are indicated as major drivers of increased mortality of target species and fisheries collapse. In scenario 1, we modeled the impacts of a disease, extreme ENSO, harmful algal blooms, or hypoxic events affecting abalone (Shepherd et al. 1998, Morales-Bojórquez et al. 2008, Micheli et al. 2012) as a negative input on abalone stock (AS; Fig. 4). Without effective effort control, a reduction in the abalone stock is accompanied by increased effort and no change in catch. However, income for both members and nonmembers is predicted to decrease, so that the increased mortality of abalone results in an overall economic loss for the local community. Biologically, the decline in abalone stocks is accompanied by a decrease in finfish stocks (FS) and an increase in lobster stocks (LS; Fig. 4). Interestingly, finfish effort is predicted to increase for both members (ME) and nonmembers (NE), but finfish catch for both groups (MC, NC) declines (Fig. 4). Job opportunities (JO) remain unaffected under all models.

In scenario 2, we modeled the negative impact of a disease on lobster stocks (Steneck et al. 2011). A negative input on lobster stock is predicted to lead to increases in abalone and no effects on finfish stocks (Fig. 2), assuming that disease would not simultaneously affect abalone and finfish stocks. The models reveal a substantial inertia of the system to lobster stock perturbation because no change is predicted for all other fishery and socioeconomic variables (Fig. 4). These simulations highlight a greater sensitivity of the system to perturbations on abalone than lobster, as suggested by more negative outcomes in scenario 1 than 2 (Fig. 4).

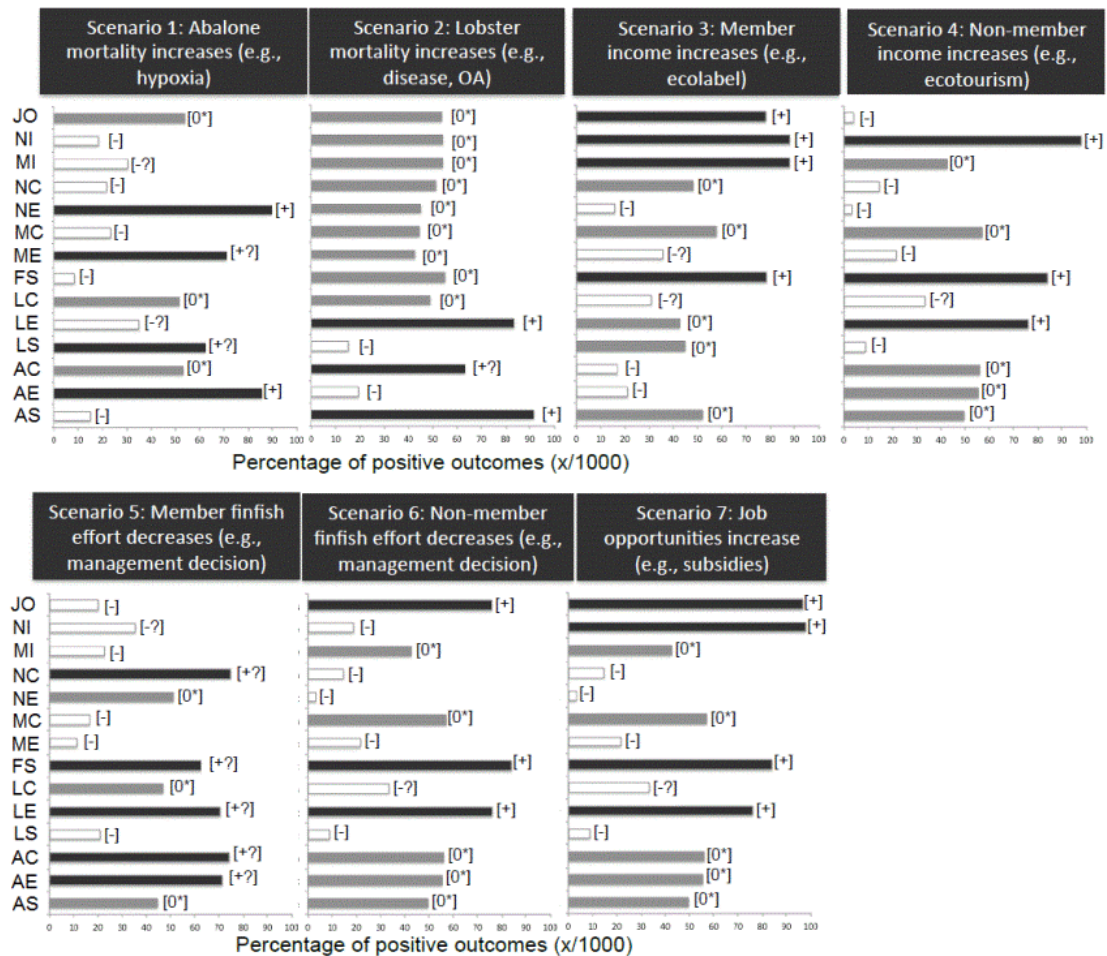
Results for scenarios 1 and 2 are relatively robust to the representation of the interactions in the system because removing links between fisheries through the effort variable does not change the directional responses of the variables (Appendix 1, Table S2).

### *Market-based interventions (scenarios 3 and 4)*

In scenario 3, we examined the effects of the ecolabel, which is represented by a positive input to member income (MI). This is the only scenario that yields predictions of positive outcomes for both biological and economic variables, and for both user groups. Income and jobs are predicted to increase for both members and nonmembers, fishing effort is expected to decrease for all fisheries, abalone and lobster stocks are predicted to remain stable, and finfish stocks to increase (Fig. 4). Thus, improving member income through market-based incentives is predicted to have beneficial effects on the overall economy, with positive consequences on stocks that are either stable (AS and LS remain unchanged) or increase (FS).

In scenario 4, nonmember income is increased through opportunities from tourism development or other income opportunities not associated with fisheries. Under this scenario, benefits would accrue only for nonmembers, whereas member income is predicted to remain unchanged. This intervention would not have an impact on the abalone fishery, as indicated by no changes in AS, AE, or AC. Finfish stocks would increase because of decreased fishing effort associated with economic

**Fig. 4.** Results from loop analysis examining the effects of external drivers and management decisions from a suite of proposed scenarios, including: (1) increased abalone mortality caused by disease or hypoxia; (2) declines in lobster stocks from disease or hypoxia; (3) increases in member income from implementation of Marine Stewardship Council (MSC) certification; (4) nonmember income increase through external opportunities (e.g., price increase); (5) management decision that leads to decrease in member finfish effort; (6) management decision that leads to decrease in nonmember finfish effort; and, (7) increase in job opportunities (e.g., from subsidies). Outcomes for each variable from each scenario are given for the main model (Model 1, Fig. 2), which includes all linkages of the social-ecological system. Bar graphs indicate the percentage of positive outcomes from the loop analysis model runs.



alternatives, and lobster stock is predicted to decrease as a result of increased abundance of their predators. Thus, the main target stocks and the overall economy are not expected to benefit under this scenario.

#### Fisheries management actions (scenarios 5, 6, 7)

Management measures put in place to reduce member effort in the finfish fishery (ME) are predicted to lead to negative socioeconomic outcomes for all user groups (scenario 5; Fig. 4). Member and nonmember incomes and jobs are all expected to decrease. Thus, economically, this scenario has the most detrimental outcome among those considered. Finfish catch by members (MC) declines whereas catch by nonmembers (NC) shows a tendency to increase. Different consequences are

predicted for abalone (AS) and lobster stocks (LS): LS is expected to decline, whereas AS is predicted not to change. Interestingly AS does not change despite both abalone effort and catch increasing. This highlights the difficulty of predicting outcomes using linear criteria of causation developed by focusing on the separate interactions between stock, effort, and catch in a single fishery.

A reduction in nonmember finfish effort (scenario 6) is also expected to result in economic loss for nonmembers and no income improvement for members. Nonmember income is predicted to decrease, likely due to finfish catch decrease because of reduced effort. Increased fish stocks result in decreased lobster stocks, whereas abalone stock is not affected and the abalone

fishery seems insensitive to this input. As finfish stock increases, the feedback within this fishery results in constant catch, even with a decrease in effort. This does not hold for nonmembers because both catch and effort decrease.

Increasing the rate of change for job opportunities (scenario 7), for example through external subsidies or investments, leads to limited beneficial effects. As in the previous case (scenario 6), nonmember income is predicted to increase whereas member income would remain stable. Again the abalone fishery seems quite unaffected by this intervention whereas negative consequences are predicted for the lobster fishery (Fig. 4).

We further varied model structure to examine potential outcomes of other management interventions that might influence the system. Specifically, in our models 1-5 we represented the more general case of effort responding to changes in catch and stock, and did not consider regulatory controls that might influence this relationship, assuming that regulatory controls may not always be effective. From trends of catch and effort data on lobster in Baja California from 1960 to 2010 (Vega 2001), two phases can be identified in the historical records. During the first period (from 1970 to approx. 1990) effort increased while catch remained more or less constant, and in the second period (from 1995 to 2004), catch increased with constant effort. Predictions from our models indicate that an increase in effort may be accompanied by a constant catch only when we simulate a negative input on lobster stock, such as increased mortality or reduction in recruitment. Outcomes that reflect the second regime, in which a constant effort was accompanied by increased catch, requires a positive input to lobster catch, which may reflect improved catchability through, for example, implementing gear changes. However, during 1995-2004, effort was kept constant in the FEDECOOP cooperatives by maintaining the number of traps and length of the fishing season constant (Vega 2001). To examine how effective control of lobster fishing effort would influence outcomes, we introduced government agency as a controlling variable on lobster effort in additional models (Appendix 1, Table S4). Government agency (GA) is introduced as an external control of LE with no self-damping and with no other links to the rest of the system, so that GA responds to and acts solely on lobster effort (Appendix 1, Fig. S1). Interestingly, the table of predictions indicates that the presence of this variable makes LE resistant to all parameter changes except for input on GA itself (Appendix 1, Table S4). Models predict that increased catch can be obtained only with a positive parameter change on lobster catch, as in the case without control over effort (Fig. 3). In this latter case, a null value represents a true zero response and not compensation due to opposite forces. This zero response is typical of variables that are connected to a satellite variable (Levins 1974, Puccia and Levins 1986). Government agency is a satellite variable because it is connected to the system only through its linkage with LE and taken in isolation represents a system with zero feedback.

#### Sensitivity analysis

The largest difference in the frequency of predicted signs among the five models considered is between models 2 and 3, which differed in 28% of all pairwise comparisons (Appendix 1, Table S3). On average, comparisons among the five models yielded different signs in 20% of cases. However, if tendencies of signs (i.e., predictions such as ?+ and ?-) are considered as true signs (i.e., ?+ becomes +

and ?- becomes -) differences are less pronounced: models 2 and 3 are still the most different but yield different predictions in only 17% of comparisons, and the average difference among models is 12%. Therefore, model structure can affect outcomes, but different predictions are obtained in a small fraction of simulations, suggesting that outcomes can be considered relatively robust to changes in the model structure that we tested.

#### DISCUSSION

Qualitative modeling approaches provide tools for learning about possible behaviors and responses to interventions in SES (Dambacher et al. 2007, Carey et al. 2014), as exemplified by this application of loop analysis to the coastal small-scale fisheries of the Vizcaino region in Baja California, Mexico. This approach can generate predictions and hypotheses about possible outcomes of management actions, new policies, or environmental drivers, and can highlight crucial links that need to be investigated to better understand the dynamics of complex SES. Loop analysis applied to the SES of coastal Baja California indicates how complex feedbacks among biological and socioeconomic components can result in counterintuitive and unexpected outcomes as a result of external perturbations. In general, our results suggest that possible trade-offs and cascading effects of management actions and new policies should be carefully considered when the goal of management is to simultaneously improve environmental condition and livelihoods of different user groups (Levin et al. 2009, Carey et al. 2014, Micheli et al. 2014a). Our results are consistent with broader scale analyses of Baja California small-scale fisheries applying the SES frameworks, which have highlighted trade-offs in achieving ecological and social sustainability, and high variability among different geographic regions of the Baja California Peninsula (e.g., Leslie et al. 2015).

Loop analysis helps highlight which components of ecosystems might be more or less vulnerable to perturbations and which interventions may be more beneficial than others for different components of the ecosystem and user groups. Our analysis of possible future scenarios of environmental or management change indicate that, under our assumptions for how system components interact, lobster stocks are predicted to be most vulnerable whereas finfish stocks are expected to benefit under most scenarios. Abalone populations appear to be generally insulated, showing relatively high resistance to changes in other components according to most scenarios. However, mass mortality of abalone (scenario 1) is predicted to have negative effects on catch and income for different user groups, with overall more negative outcomes than, e.g., disease or environmental conditions causing lobster mortality. In other words, abalone stock is rather insensitive to changes in other variables but changes in abalone's rate of change are likely to influence the whole system. Our models also show a negative correlation between lobster and finfish stocks. This negative correlation suggests that attempts to restore one of the two stocks or increasing its growth rate will negatively affect the other unless interventions are targeted to few variables (i.e., AC, LS, LC, ME, MI). These hypotheses need to be tested and should be carefully considered before management intervention.

Models produced specific predictions about the possible socioeconomic outcomes of different interventions or perturbations, and highlight what management interventions might be most beneficial or most detrimental to the local economy.



Only scenario 3, the ecolabel, shows positive effects on all three socioeconomic variables considered, i.e., member and nonmember income and jobs. The other six scenarios yield less positive outcomes for the economy of the system, where most predictions are negative (e.g., mass mortality affecting abalone stocks, the most valuable resource in this system, and a reduction of finfish effort within the cooperative) or show no consistent change (e.g., mass mortality affecting lobster, for which the cooperative, as for abalone, holds exclusive access rights). Thus, in this system, among the management interventions considered, the ecolabel is expected to have the greatest benefits whereas a reduction in finfishing effort by cooperative members the most detrimental. Moreover, the economic impacts of a mass mortality event of abalones are predicted to be greater than in the case of lobster.

Other studies conducted in this region have documented differential performance of fishers and fisheries in the face of change in environmental conditions. For example, Finkbeiner (2014) found that diversification of fishing activities was important for risk mitigation and stabilizing income, but the ability to specialize on high-value species during favorable conditions resulted in wealth accumulation. Thus, the flexibility to move across fishing strategies given changing environmental conditions is important for the adaptive capacity of small-scale fishing cooperatives. Further research on SES of Baja California and other regions should account for these dynamic responses to change, and how different governance frameworks and markets may enable or constrain adaptation.

Models also highlight what user groups might be more vulnerable to external shocks. In this SES, nonmember income is more sensitive than member income to environmental variability or the management decisions considered in these scenarios (Fig. 4; Appendix 1, Table S2). Interestingly, member income shows resistance to change when the system is perturbed through inputs that affect nonmembers, such as finfish stock, nonmember income, nonmember effort on finfish, nonmember catch, and job opportunities. Should these conclusions survive further scrutiny, they would indicate how management decisions might affect these communities because costs and benefits may be unevenly distributed. This is particularly important as perceived inequity in resource access, illegitimacy of process, and loss of social capital can influence how people comply with regulations, and, if ignored, can lead to unintended consequences, such as increased poaching and declines in species abundance (McClanahan et al. 2009). Ultimately, this can lead to poverty traps and affect the adaptive capacity of SES (Cinner 2011). An important next step will be to conduct in-depth analyses and modeling of social dynamics and possible unintended consequences of interventions in this and other coastal SES (e.g., Finkbeiner 2014). It is important to recognize that governance approaches addressing problems in one SES dimension could trigger unintended consequences in other dimensions if issues are not addressed in the whole system perspective. A comprehensive, integrative understanding of SES in this and other systems will enable sustainability science to more fully inform sustainability practice (Leslie et al. 2015).

Loop analysis can also reveal important potential trade-offs between desirable ecological and social outcomes, and can help

identify which interventions may instead lead to potential win-win outcomes. In this case study, for example, management interventions, such as additional finfish fisheries regulation, are expected to have negative economic impacts, whereas creating new jobs through ecotourism or subsidies might have mixed effects on cooperative members versus nonmembers. Market interventions, like the ecolabel, are expected to have overall positive economic effects. Moreover, this positive economic impact is associated with a lack of negative biological impacts under most model structures, indicating that this market-based intervention poses the least trade-offs among those considered. Furthermore, under this scenario, the benefits are distributed across multiple stakeholder groups, in which both members and nonmembers are predicted to thrive. However, we caution applying outcomes from loop analysis without further modeling or empirical support for at least a core set of the variables. For example, our assumption that an ecolabel automatically increases the rate of change of member income may not be applicable in all systems. Although ecolabels can influence market price and increase income, and did result in documented benefits for FEDECOOP cooperative members and nonmembers in this region (Pérez-Ramírez et al. 2012b), this is highly dependent on access to markets, infrastructure, and processing capabilities (Pérez-Ramírez et al. 2012a).

Loop analysis can identify what pathways may have greater influence on the outcomes, highlighting potentially important relationships to examine in future research and analysis. As described in our results, loop analysis may predict both expected and unexpected outcomes. For example, in this case study loop analysis predicts that an increase of fish stock abundance (FS) has a negative effect on the growth rate of its lobster (LS) but not abalone (AS) prey. As in any network analysis of complex systems, multiple pathways mediate the effects of one variable on another, so the full set of pathways must be examined to understand the effects. In each case (links from FS to LS and from FS to AS), there are multiple pathways carrying opposite effects, i.e., negative and positive. Thus, if only the number of pathways influenced the outcome of the loop analysis, we would expect the results of the simulation to lead to a neutral effect of FS on both AS and LS. Likely this discrepancy between what we would expect based on the number of pathways and what we obtain from the simulations depends on the fact that the product of link values, drawn from a random distribution, can yield small numbers in longer paths whereas the shorter paths tend to drive the final outcome of the loop analysis. In the example discussed above, the shortest paths are both negative from FS to LS but one positive and one negative from FS to AS.

This case study exemplifies the potential of loop analysis in SES applications and highlights the remaining weaknesses and caveats of this approach. In loop analysis, similar to other modeling approaches, predictions are strongly dependent on the specific assumptions about the relevant components of the SES, the nature of the linkages among these components, and the overall structure of the network. A major source of uncertainty is associated with our still limited ability to accurately represent the relationships between the variables. Although our depiction of the social-ecological system of the Vizcaino fisheries and decisions about the nature and direction of interactions are based on available knowledge of this and other similar systems, high uncertainty remains. For example, the observed negative impacts on lobster



stocks that we obtained in several simulations are likely because of the assumption that predation by some finfish taxa (e.g., sheephead, which is targeted by local fisheries) controls lobster stocks. Although sheephead are major predators of lobster and sheephead control of benthic invertebrate populations has been demonstrated in kelp forests of southern California (Cowen 1983), there is no empirical evidence for top-down predatory control of lobster populations along the coast of Baja California.

Increasing the reliability of predictions can be obtained by designing alternative network structures and assessing the robustness of predictions to these different depictions of the linkages. This can help identify which structural differences matter. For example the abalone fishery subsystem (Fig. 3, columns labeled AS, AE, AC) appears to be quite resistant to environmental change. Of the 5 alternative network structures that we analyzed, 22 or more of the 42 predictions related to this subsystem show no response to parameter change (Appendix 1, Table S2). This robust outcome may be the effect of a core structure common to all models upon which few links added or removed do not change the predictions. Thus, it is particularly important that the core structure of models is carefully constructed, integrating all available sources of information and input from different stakeholders. In fact, an important benefit of loop analysis is that it provides a framework for integrating different types of information, thereby offering an opportunity to involve stakeholders in participatory model construction (Anthony et al. 2013). Both for qualitative and quantitative modeling approaches, model development will benefit from implementing participatory frameworks, in which different types of knowledge of the system from different users are included and tested to determine what variables and linkages are most relevant to the outcomes (Essington et al. 2016, Stier et al. 2016).

Our results, besides specific predictions in the different scenarios, highlight that patterns of correlation depend on the network structure and the entry point of the perturbation. For example, abalone (AS) and lobster stocks (LS) are negatively correlated with one another when biological stress enters the system (scenarios 1 and 2). However, when a press perturbation affects nonbiological variables (effort, income, job opportunities, scenarios from 2 to 7), the two stocks appear uncorrelated with one another. It follows that patterns of correlation from field data can be used to detect the entry points of perturbation in the system, and this highlights the potential of loop analysis as a diagnostic tool.

Loop analysis has been used in a few other cases of scenario analysis in the context of fishery (Anthony et al. 2013, Espinoza-Tenorio et al. 2013, Carey et al. 2014, Dambacher et al. 2015). Nevertheless, this technique presents several limitations that must be carefully addressed in management contexts. Justus (2006) outlined what outcomes from loop analysis are with regard to changes in the equilibrium level of the variables, but real systems are generally not at equilibrium, and nonlinearities often characterize variables' dynamics. Although previous studies (Lane and Collins 1985, Bodini 1988, 2000) have offered evidence that loop analysis can be applied to dynamic systems by considering changes in average values of the variables, dynamic changes remain a main challenge for qualitative modeling techniques. Another limitation of loop analysis concerns the time

scale at which predicted effects may manifest themselves. For example, change can occur gradually, over long time frames, for some components of SES whereas others may experience sudden shifts. Variables that belong to different domains may show very different dynamics, thus time scales must be carefully considered and directly addressed by combining qualitative analysis and quantitative dynamic models.

Other qualitative modeling approaches can offer some advantages with respect to loop analysis. For example, fuzzy cognitive maps (FCMs) make the magnitude of links explicit through a semiquantification of the relationships between the variables (Özesmi and Özesmi 2004, Kok 2009). This approach resolves the ambiguities about the net effect of contrasting pathways discussed above. Another advantage of FCM over loop analysis is that it can make predictions about multiple simultaneous perturbations. However, the procedure for constructing FCMs requires experts to describe the structure and the interconnections of the network using fuzzy conditional (IF-THEN) statements. Such statements are of the type "if the level of variable A is high, that of variable B is low." This implies that experts define the relationships from correlations between the variables derived from observing the system (Stylios and Groumpos 1999). Our results highlight that patterns of correlation depend on the network structure and the entry point of the perturbation. For example, abalone (AS) and lobster stocks (LS) are negatively correlated with one another when biological stress enters the system through mass mortalities (scenarios 1 and 2). However, when perturbations affect the system through nonbiological variables (e.g., changes in effort, income, and job opportunities, scenarios 2-7), the two stocks appear uncorrelated with one another. It follows that defining interactions on the base of their correlations may be misleading (Levins and Puccia 1988).

Both loop analysis and FCMs allow for predicting changes in the level of the variables in a complex system following a perturbation to one of them. However, an advantage of loop analysis is that it models the effect of a perturbation to the rate of change of a variable, which isn't dependent on the initial state of the variable. For example, in scenario 1, we investigated the effect of an increased mortality of abalones due to climate change. Although we can expect heat waves and/or hypoxia to increase the mortality of abalone populations, based on available data (Morales-Bojórquez et al. 2008, Micheli et al. 2012), it is more difficult to predict the resulting abundance. In FCMs, instead, the perturbation is simulated as a change in the initial state of one or more variables (i.e., the abundance of a population), but changes in the level of the variables are difficult to predict (Levins and Puccia 1988). Therefore, in our case, loop analysis is more appropriate because it allows the incorporation of disturbances based on the knowledge of the direction of the variables' rates of change (negative, neutral, or positive). Given the strengths and weaknesses of each approach, there is great potential for fruitful integrations as shown by Ramsey and Veltman (2005).

Other qualitative modeling approaches include causal loop diagrams (CLD; Richardson 1986) and Bayesian belief networks (BBN; Borsuk et al. 2004; Pollino et al. 2007). Causal loop diagrams make predictions by logically reconstructing the causal chains of causes and effects between the variables on the basis of link polarities. However, predicting the behavior of complex

networks, such as the one examined here, by identifying the feedback effects using link polarity is difficult and can lead to misleading interpretations of the effects, as previously highlighted by Richardson (1986). Similarly, specifying the relevant conditional probabilities as required by BBN can be a laborious and time-consuming process (Ticehurst et al. 2007). Moreover, including feedbacks via cyclic network structures requires dynamic time-explicit BBNs that depend on extensive parameterization. Hence, BBNs do not usually include feedbacks common to ecological systems (Marcot et al. 2001). Similar to FCMs, combining BBNs with loop analysis has great potential for improving predictions and model validation (Melbourne-Thomas et al. 2012, Anthony et al. 2013). However it must be emphasized that these applications of BBNs are based on the signs derived from the analysis of the qualitative models. As such, their outcomes are contingent on the assumptions and limitations of the signed diagram models.

## CONCLUSION

Managing fisheries under an ecosystem-based approach requires a shift in focus from single fisheries and sectors to a comprehensive strategy in which management considers multiple fisheries, multiple species, multiple aspects of local communities, and their linkages. Only by taking a holistic view of the SES can we begin to predict the consequences of multiple human activities, management interventions, and environmental shocks. Qualitative modeling approaches allow managers, stakeholders, and scientists to examine which of a suite of possible interventions has the greatest potential to influence other biological and socioeconomic components in the system, and which are more resistant to change. Furthermore, models and their outcomes can help identify key components and linkages, and prioritize data collection and management actions. However, qualitative models including loop analysis are subject to high uncertainty and outcomes of model perturbations are contingent on the assumptions about structural linkages. As such, qualitative models should be tested with empirical data and combined with quantitative dynamic models to increase certainty around model predictions. Despite their limitations, qualitative models that include linkages across the SES are integral to a comprehensive, system-wide approach that addresses ecological integrity, intergenerational opportunities, and economic efficiency, three key dimensions of the sustainable development paradigm.

Responses to this article can be read online at:  
<http://www.ecologyandsociety.org/issues/responses.php/8825>

## Acknowledgments:

This work was supported by NSF grants (OCE-0410439 and DEB-1212124) and a grant from the Packard Foundation's Conservation and Science Program. We thank B. McCay, G. Shester, S. Lluch, G. Ponce, S. Guzman del Proo, E. Serviere, D. Aguilar, M. Valenzuela, and several members of the cooperatives "Progreso" and "Punta Abreojos" for their advice and support. Thanks to Stefania Favilla (University of Modena-Reggio Emilia, Italy) who developed the first version of the algorithm that computes

loop-analysis predictions through simulations. Two anonymous reviewers and Dr. Kasper Kok greatly contributed to improving this article.

## LITERATURE CITED

- Anthony, K. R. N., J. M. Dambacher, T. Walshe, and R. A. Beeden. 2013. *A framework for understanding cumulative impacts, supporting environmental decisions and informing resilience-based management of the Great Barrier Reef World Heritage Area*. Australian Institute of Marine Science, Townsville, Australia; CSIRO, Hobart, Australia; NERP Decisions Hub, University of Melbourne and Great Barrier Reef Marine Park Authority, Townsville, Australia. [online] URL: [https://www.environment.gov.au/system/files/resources/2910cf7e-30fc-466f-a6c1-0e27aa618d05/files/framework-resilience-based-management\\_0.pdf](https://www.environment.gov.au/system/files/resources/2910cf7e-30fc-466f-a6c1-0e27aa618d05/files/framework-resilience-based-management_0.pdf)
- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65:1-13. <http://dx.doi.org/10.2307/1939452>
- Berkes, F. 2006. From community-based resource management to complex systems: the scale issue and marine commons. *Ecology and Society* 11(1):45. <http://dx.doi.org/10.5751/ES-01431-110145>
- Berkes, F. 2011. Restoring unity: the concept of marine social-ecological systems. Pages 9-28 in R. E. Ommer, R. I. Perry, K. Cochrane, and P. Cury, editors. *World fisheries: a social-ecological analysis*. Wiley-Blackwell, Oxford, UK. <http://dx.doi.org/10.1002/9781444392241.ch2>
- Berkes, F., and C. Folke. 1998. Linking sociological and ecological systems: management practices and social mechanisms for building resilience. Cambridge University Press, New York, New York, USA.
- Bodini, A. 1988. Representing ecosystem structure through signed digraphs. Model reconstruction, qualitative predictions and management: the case of a freshwater ecosystem. *Oikos* 83:93-106. <http://dx.doi.org/10.2307/3546550>
- Bodini, A. 2000. Reconstructing trophic interactions as a tool for understanding and managing ecosystems: application to a shallow eutrophic lake. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1999-2009. <http://dx.doi.org/10.1139/f00-153>
- Borsuk, M. E., C. A. Stow, and K. H. Reckhow. 2004. A Bayesian network of eutrophication models for synthesis, prediction, and uncertainty analysis. *Ecological Modelling* 173:219-239. <http://dx.doi.org/10.1016/j.ecolmodel.2003.08.020>
- Boumans, R., and R. Costanza. 2007. The multiscale integrated Earth Systems model (MIMES): the dynamics, modeling and valuation of ecosystem services. Pages 104-107 in *GWSP issues in global water system research report*. Federal Ministry of Education and Research, Global Water System Project, Bonn, Germany. [online] URL: [https://www.pdx.edu/sites/www.pdx.edu/sustainability/files/Boumans\\_Costanza\\_GWSP%20Chapter\\_2007.pdf](https://www.pdx.edu/sites/www.pdx.edu/sustainability/files/Boumans_Costanza_GWSP%20Chapter_2007.pdf)
- Braje, T. J., J. M. Erlandson, T. C. Rick, P. K. Dayton, and M. B. A. Hatch. 2009. Fishing from past to present: continuity and resilience of red abalone fisheries on the Channel Islands, California. *Ecological Applications* 19(4):906-919. <http://dx.doi.org/10.1890/08-0135.1>

- Carey, M. P., P. S. Levin, H. Townsend, T. J. Minello, G. R. Sutton, T. Francis, C. J. Harvey, J. E. Toft, K. K. Arkema, J. L. Burke, C.-K. Kim, A. Guerry, M. Plummer, G. Spiridonov, and M. Ruckelshaus. 2014. Characterizing coastal foodwebs with qualitative links to bridge the gap between the theory and the practice of ecosystem-based management. *ICES Journal of Marine Science* 71(3):713-724. <http://dx.doi.org/10.1093/icesjms/fst012>
- Cinner, J. E. 2011. Social-ecological traps in reef fisheries. *Global Environmental Change* 21(3):835-839. <http://dx.doi.org/10.1016/j.gloenvcha.2011.04.012>
- Costello, C., S. Gaines, and J. Lynham. 2008. Can catch shares prevent fisheries collapse? *Science* 321:1678-1681. <http://dx.doi.org/10.1126/science.1159478>
- Cowen, R. K. 1983. The effect of sheephead (*Semicossyphus pulcher*) predation on red sea urchin (*Strongylocentrotus franciscanus*) populations: an experimental analysis. *Oecologia* 58 (2):249-255. <http://dx.doi.org/10.1007/bf00399225>
- Cox, M., G. Arnold, and S. Villamayor Tómas. 2010. A review of design principles for community-based natural resource management. *Ecology and Society* 15(4):38. [online] URL: <http://www.ecologyandsociety.org/vol15/iss4/art38/>
- Dambacher, J. M., D. T. Brewer, D. M. Dennis, M. Macintyre, and S. Foale. 2007. Qualitative modelling of gold mine impacts on Lihir Island's socioeconomic system and reef-edge fish community. *Environmental Science and Technology* 41:555-562. <http://dx.doi.org/10.1021/es0610333>
- Dambacher, J. M., P. C. Rothlisberg, and N. R. Loneragan. 2015. Qualitative mathematical models to support ecosystem-based management of Australia's northern prawn fishery. *Ecological Applications* 25:278-298. <http://dx.doi.org/10.1890/13-2030.1>
- Defeo, O., and J. C. Castilla. 2012. Governance and governability of coastal shellfisheries in Latin America and the Caribbean: multi-scale emerging models and effects of globalization and climate change. *Current Opinion in Environmental Sustainability* 4:344-350. <http://dx.doi.org/10.1016/j.cosust.2012.05.002>
- Espinoza-Tenorio, A., M. Wolff, I. Espejel, and G. Montaña-Moctezuma. 2013. Using traditional ecological knowledge to improve holistic fisheries management: transdisciplinary modeling of a lagoon ecosystem of southern Mexico. *Ecology and Society* 18(2):6. <http://dx.doi.org/10.5751/es-05369-180206>
- Essington, T. E., L. Ciannelli, S. S. Heppell, P. S. Levin, T. R. McClanahan, F. Micheli, É. E. Plagányi, and I. E. van Putten. 2016. Empiricism and modeling for marine fisheries: advancing an interdisciplinary science. *Ecosystems* :1-8. <http://dx.doi.org/10.1007/s10021-016-0073-0>
- Finkbeiner, E. 2014. *Survival and sustainability in small-scale Mexican fisheries: a cross-scale examination of resilience in marine social-ecological system*. Dissertation. Stanford University, Stanford, California, USA. [online] URL: <https://searchworks.stanford.edu/view/10701355>
- Fishwick, P. A., and P. A. Luker. 1991. *Qualitative simulation modeling and analysis*. Springer-Verlag, New York, New York, USA. <http://dx.doi.org/10.1007/978-1-4613-9072-5>
- Fulton, E. A., J. S. Link, I. C. Kaplan, M. Savina-Rolland, P. Johnson, C. Ainsworth, P. Horne, R. Gorton, R. J. Gamble, A. D. M. Smith, and D. C. Smith. 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries* 12(2):171-188. <http://dx.doi.org/10.1111/j.1467-2979.2011.00412.x>
- Halpern, B. S., C. Longo, D. Hardy, K. L. McLeod, J. F. Samhour, S. K. Katona, K. Kleisner, S. E. Lester, J. O'Leary, M. Ranelletti, A. A. Rosenberg, C. Scarborough, E. R. Selig, B. D. Best, D. R. Brumbaugh, F. S. Chapin, L. B. Crowder, K. L. Daly, S. C. Doney, C. Elfes, M. J. Fogarty, S. D. Gaines, K. I. Jacobsen, L. B. Karrer, H. M. Leslie, E. Neeley, D. Pauly, S. Polasky, B. Ris, K. St Martin, G. S. Stone, U. R. Sumaila, and D. Zeller. 2012. An index to assess the health and benefits of the global ocean. *Nature* 488:615-620. <http://dx.doi.org/10.1038/nature11397>
- Hughes, T. P., D. R. Bellwood, C. Folke, R. S. Steneck, and J. Wilson. 2005. New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology and Evolution* 20 (7):380-386. <http://dx.doi.org/10.1016/j.tree.2005.03.022>
- Kittinger, J. N., E. M. Finkbeiner, N. C. Ban, K. Broad, M. H. Carr, J. E. Cinner, S. Gelcich, M. L. Cornwell, J. Z. Koehn, X. Basurto, R. Fujita, M. R. Caldwell, and L. B. Crowder. 2013. Emerging frontiers in social-ecological systems research for sustainability of small-scale fisheries. *Current Opinion in Environmental Sustainability* 5:352-357. <http://dx.doi.org/10.1016/j.cosust.2013.06.008>
- Kok, K. 2009. The potential of Fuzzy Cognitive Maps for semi-quantitative scenario development, with an example from Brazil. *Global Environmental Change* 19:122-133. <http://dx.doi.org/10.1016/j.gloenvcha.2008.08.003>
- Justus, J. 2006. Loop analysis and qualitative modeling: limitations and merits. *Biology and Philosophy* 21:647-666. <http://dx.doi.org/10.1007/s10539-006-9050-x>
- Lane, D. C. 2008. The emergence and use of diagramming in system dynamics: a critical account. *Systems Research and Behavioral Science* 25:3-23. <http://dx.doi.org/10.1002/sres.826>
- Lane, P., and T. M. Collins. 1985. Food web models of a marine plankton community network: an experimental mesocosm approach. *Journal of Experimental Marine Biology and Ecology* 94:41-70. [http://dx.doi.org/10.1016/0022-0981\(85\)90049-8](http://dx.doi.org/10.1016/0022-0981(85)90049-8)
- Leslie, H. M., X. Basurto, M. Nenadovic, L. Sievanen, K. C. Cavanaugh, J. J. Cota-Nieto, B. E. Erisman, E. Finkbeiner, G. Hinojosa-Arango, M. Moreno-Báez, S. Nagavarapu, S. M. W. Reddy, Sánchez-Rodríguez, K. Siegel, J. Ulibarria-Valenzuela, A. Hudson Weaver, and O. Aburto-Oropeza. 2015. Operationalizing the social-ecological systems framework to assess sustainability. *Proceedings of the National Academy of Sciences* 112 (19):5979-5984. <http://dx.doi.org/10.1073/pnas.1414640112>
- Leslie, H. M., and K. L. McLeod. 2007. Confronting the challenges of implementing marine ecosystem-based management. *Frontiers in Ecology and the Environment* 5(10):540-548. <http://dx.doi.org/10.1890/060093>
- Levin, P. S., M. J. Fogarty, S. A. Murawski, and D. Fluharty. 2009. Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. *PLoS Biology* 7 (1):e1000014. <http://dx.doi.org/10.1371/journal.pbio.1000014>



- Levins, R. 1974. Discussion paper: the qualitative analysis of partially specified systems. *Annals of the New York Academy of Science* 231:123-138. <http://dx.doi.org/10.1111/j.1749-6632.1974.tb20562.x>
- Levins, R., and C. J. Puccia. 1988. The controlling factor in biological communities. *Coenoses* 3(3):149-154.
- Mahon, R., P. McConney, and R. N. Roy. 2008. Governing fisheries as complex adaptive systems. *Marine Policy* 32:104-112. <http://dx.doi.org/10.1016/j.marpol.2007.04.011>
- Marcot, B. G., R. S. Holthausen, M. G. Raphael, M. M. Rowland, and M. J. Wisdom. 2001. Using Bayesian belief networks to evaluate fish and wildlife population viability under land management alternatives from an environmental impact statement. *Forest Ecology and Management* 153:29-42. [http://dx.doi.org/10.1016/S0378-1127\(01\)00452-2](http://dx.doi.org/10.1016/S0378-1127(01)00452-2)
- Martone, R. L. G. 2009. *Geographic variation in species demography and community structure in temperate rocky reefs*. Dissertation. Stanford University, Stanford, California, USA. [online] URL: <http://gradworks.umi.com/33/51/3351489.html>
- McCay, B. J., F. Micheli, G. Ponce-Díaz, G. Murray, G. Shester, S. Ramirez-Sanchez, and W. Weisman. 2014. Cooperatives, concessions, and co-management on the Pacific coast of Mexico. *Marine Policy* 44:49-59. <http://dx.doi.org/10.1016/j.marpol.2013.08.001>
- McClanahan, T. R., J. C. Castilla, A. T. White, and O. Defeo. 2009. Healing small-scale fisheries by facilitating complex socio-ecological systems. *Reviews in Fish Biology and Fisheries* 19:33-47. <http://dx.doi.org/10.1007/s11160-008-9088-8>
- McGinnis, M. D., and E. Ostrom. 2014. Social-ecological system framework: initial changes and continuing challenges. *Ecology and Society* 19(2):30. <http://dx.doi.org/10.5751/es-06387-190230>
- McLeod, K. L., J. Lubchenco, S. R. Palumbi, and A. A. Rosenberg. 2005. *Scientific consensus statement on marine ecosystem-based management*. Compass, Corvallis, Oregon, USA. [online] URL: [http://www.compassonline.org/science/EBM\\_CMSP/EBMconsensus](http://www.compassonline.org/science/EBM_CMSP/EBMconsensus)
- Melbourne-Thomas, J., S. Wotherspoon, B. Raymond, and A. Constable. 2012. Comprehensive evaluation of model uncertainty in qualitative network analyses. *Ecological Monographs* 82:505-519. <http://dx.doi.org/10.1890/12-0207.1>
- Micheli, F., G. De Leo, C. Butner, R. G. Martone, and G. Shester. 2014b. A risk-based framework for assessing the cumulative impact of multiple fisheries. *Biological Conservation* 176:224-235. <http://dx.doi.org/10.1016/j.biocon.2014.05.031>
- Micheli, F., G. De Leo, G. G. Shester, R. G. Martone, S. E. Lluch-Cota, C. Butner, L. B. Crowder, R. Fujita, S. Gelcich, M. Jain, S. E. Lester, B. McCay, R. Pelc, and A. Sáenz-Arroyo. 2014a. A system-wide approach to supporting improvement in seafood production practices and outcomes. *Frontiers in Ecology and the Environment* 12:297-305. <http://dx.doi.org/10.1890/110257>
- Micheli, F., A. Saenz-Arroyo, A. Greenley, L. Vazquez, J. A. E. Montes, M. Rossetto, and G. A. De Leo. 2012. Evidence that marine reserves enhance resilience to climatic impacts. *PLoS One* 7(7):e40832. <http://dx.doi.org/10.1371/journal.pone.0040832>
- Montoya, J. M., G. Woodward, M. C. Emmerson, and R. V. Solé. 2009. Indirect effects propagate disturbances in real food webs. *Ecology* 90:2426-2433. <http://dx.doi.org/10.1890/08-0657.1>
- Morales-Bojórquez, E., M. O. Muciño-Díaz, and J. A. Vélez-Barajas. 2008. Analysis of the decline of the abalone fishery (*Haliotis fulgens* and *H. corrugata*) along the west-central coast of the Baja California Peninsula, Mexico. *Journal of Shellfish Research* 27:865-870. [http://dx.doi.org/10.2983/0730-8000\(2008\)27\[865:AOTDOT\]2.0.CO;2](http://dx.doi.org/10.2983/0730-8000(2008)27[865:AOTDOT]2.0.CO;2)
- Morales-Zárate, M. V., S. E. Lluch-Cota, E. Serviere-Zaragoza, and S. Guzmán del Próo. 2011. Modeling an exploited rocky coastal ecosystem: Bahía Tortugas, Mexico. *Ecological Modelling* 222:1185-1191. <http://dx.doi.org/10.1016/j.ecolmodel.2010.12.011>
- Nelson, E., G. Mendoza, J. Regetz, S. Polasky, H. Tallis, D. R. Cameron, K. M. A. Chan, G. C. Daily, J. Goldstein, P. M. Kareiva, E. Lonsdorf, R. Naidoo, T. H. Ricketts, and M. R. Shaw. 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Frontiers in Ecology and the Environment* 7:4-11. <http://dx.doi.org/10.1890/080023>
- Ostrom, E. 2009. A general framework for analyzing sustainability of social-ecological systems. *Science* 325 (5939):419-422. <http://dx.doi.org/10.1126/science.1172133>
- Özesmi, U., and S. L. Özesmi. 2004. Ecological models based on people's knowledge: a multi-step Fuzzy Cognitive Mapping approach. *Ecological Modelling* 176:43-64. <http://dx.doi.org/10.1016/j.ecolmodel.2003.10.027>
- Peckham, S. H., D. Maldonado Diaz, A. Walli, G. Ruiz, L. B. Crowder, and W. J. Nichols. 2007. Small-scale fisheries bycatch jeopardizes endangered Pacific loggerhead turtles. *PLoS One* 2 (10):e1041. <http://dx.doi.org/10.1371/journal.pone.0001041> CHECK
- Pérez-Ramírez, M., M. A. Almendarez-Hernandez, G. Aviles-Polanco, and L. F. Beltran-Morales. 2015. Consumer acceptance of eco-labeled fish: a Mexican case study. *Sustainability* 7 (4):4625-4642.
- Pérez-Ramírez, M., B. Phillips, D. Lluch-Belda, and S. Lluch-Cota. 2012a. Perspectives for implementing fisheries certification in developing countries. *Marine Policy* 36:297-302. <http://dx.doi.org/10.1016/j.marpol.2011.06.013>
- Pérez-Ramírez, M., G. Ponce-Díaz, and S. Lluch-Cota. 2012b. The role of MSC certification in the empowerment of fishing cooperatives in Mexico: the case of red rock lobster co-managed fishery. *Ocean and Coastal Management* 63:24-29. <http://dx.doi.org/10.1016/j.ocecoaman.2012.03.009>
- Pollino, C. A., O. Woodberry, A. Nicholson, K. Korb, and B. T. Hart. 2007. Parameterization and evaluation of a Bayesian network for use in an ecological risk assessment. *Environmental Modelling and Software* 22:1140-1152. <http://dx.doi.org/10.1016/j.envsoft.2006.03.006>
- Pomeroy, R. S., B. M. Katon, and I. Harkes. 2001. Conditions affecting the success of fisheries co management: lessons from Asia. *Marine Policy* 25:197-208. [http://dx.doi.org/10.1016/S0308-597X\(01\)00010-0](http://dx.doi.org/10.1016/S0308-597X(01)00010-0)



- Ponce-Díaz, G., A. Vega-Velázquez, M. Ramade-Villanueva, G. Leon-Carballo, and R. Franco-Santiago. 1998. Socioeconomic characteristics of the abalone fishery along the west coast of the Baja California peninsula, Mexico. *Journal of Shellfish Research* 17(3):853-857.
- Ponce-Díaz, G., W. Weisman, and B. McCay. 2009. Co-responsibility and participation in fisheries management in Mexico: lessons from Baja California Sur. *Pesca y Conservación* 1:1-9.
- Puccia, C. J., and R. Levins. 1986. *Qualitative modeling of complex systems: an introduction to loop analysis and time averaging*. Harvard University Press, Cambridge, Massachusetts, USA. <http://dx.doi.org/10.4159/harvard.9780674435070>
- Ramírez Sánchez, S., B. J. McCay, T. R. Johnson, and W. Weisman. 2011. Surgimiento, formación y persistencia de organizaciones sociales para la pesca ribereña de la península de Baja California. *Región y Sociedad* 23(51):71-99.
- Ramsey, D., and C. Veltman. 2005. Predicting the effects of perturbations on ecological communities: what can qualitative models offer? *Journal of Animal Ecology* 74:905-916. <http://dx.doi.org/10.1111/j.1365-2656.2005.00986.x>
- Reum, J. C. P., P. S. McDonald, B. E. Ferriss, D. M. Farrell, C. J. Harvey, and P. S. Levin. 2015. Qualitative network models in support of ecosystem approaches to bivalve aquaculture *ICES Journal of Marine Science* 72(8):2278-2288. <http://dx.doi.org/10.1093/icesjms/fsv119>
- Richardson, G. P. 1986. Problems with causal-loop diagrams. *System Dynamics Review* 2:158-170. <http://dx.doi.org/10.1002/sdr.4260020207>
- Schlager, E., and E. Ostrom. 1992. Property-rights regimes and natural resources: a conceptual analysis. *Land Economics* 68 (3):249-262. <http://dx.doi.org/10.2307/3146375>
- Shepherd, S. A., J. R. Turrubiates-Morales, and K. Hall. 1998. Decline of the abalone fishery at La Natividad, Mexico: overfishing or climate change? *Journal of Shellfish Research* 17:839-846.
- Shester, G. G. 2008. *Sustainability in small-scale fisheries: an analysis of ecosystem impacts, fishing behaviour, and spatial management using participatory research methods*. Dissertation. Stanford University, Stanford, California, USA. [online] URL: <http://gradworks.umi.com/33/32/3332993.html>
- Shester, G. G., and F. Micheli. 2011. Conservation challenges for small-scale fisheries: bycatch and habitat impacts of traps and gillnets. *Biological Conservation* 144:1673-1681. <http://dx.doi.org/10.1016/j.biocon.2011.02.023>
- Steneck, R. S., T. P. Hughes, J. E. Cinner, W. N. Adger, S. N. Arnold, F. Berkes, S. A. Boudreau, K. Brown, C. Folke, L. Gunderson, P. Olsson, M. Scheffer, E. Stephenson, B. Walker, J. Wilson, and B. Worm. 2011. Creation of a gilded trap by the high economic value of the Maine lobster fishery. *Conservation Biology* 25:904-912. <http://dx.doi.org/10.1111/j.1523-1739.2011.01717.x>
- Stier, A. C., J. F. Samhouri, S. Gray, R. G. Martone, M. E. Mach, B. S. Halpern, C. V. Kappel, C. Scarborough, and P. S. Levin. 2016. Integrating expert perceptions into food web conservation and management. *Conservation Letters*. <http://dx.doi.org/10.1111/conl.12245>
- Stylios, C. D., and P. P. Groumpos. 1999. A soft computing approach for modelling the supervisor of manufacturing systems. *Journal of Intelligent and Robotic Systems* 26:389-403. <http://dx.doi.org/10.1023/A:1008165916707>
- Ticehurst, J. L., L. T. H. Newham, D. Rissik, R. A. Letcher, and A. J. Jakeman. 2007. A Bayesian network approach for assessing the sustainability of coastal lakes in New South Wales, Australia. *Environmental Modelling and Software* 22:1129-1139. <http://dx.doi.org/10.1016/j.envsoft.2006.03.003>
- Vega, V. A. 2001. *Dinamica poblacional y evaluación de la langosta roja (Panulirus interruptus) en la zona central de la península Baja California e indicadores de la pesquería regional*. Informe de Investigación, Centro Regional de Investigación Pesquera-La Paz Instituto Nacional de la Pesca, Mexico.
- Whiteley, N. M. 2011. Physiological and ecological responses of crustaceans to ocean acidification. *Marine Ecology Progress Series* 430:257-271. <http://dx.doi.org/10.3354/meps09185>
- Wooldridge, S., and T. Done. 2004. Learning to predict large-scale coral bleaching from past events: a Bayesian approach using remotely sensed data, in-situ data, and environmental proxies. *Coral Reefs* 23:96-108. <http://dx.doi.org/10.1007/s00338-003-0361-y>
- Wootton, J. T. 2002. Indirect effects in complex ecosystems: recent progress and future challenges. *Journal of Sea Research* 48:157-172. [http://dx.doi.org/10.1016/S1385-1101\(02\)00149-1](http://dx.doi.org/10.1016/S1385-1101(02)00149-1)

## Appendix S-A

### Loop analysis: making predictions through signed digraphs

In what follows, we are showing how the loop analysis algorithm for predictions works using a simple model. In Figure S1 a simple tri-trophic linear chain comprises a resource (A), an intermediate consumer (B) and a final consumer (C). Loop analysis considers variations in the level of the variables as consequences of perturbations that permanently alter the rate of change of the variable. Suppose that  $c$  is the mortality of species A. If  $c$  is reduced (e.g. because of improved environmental conditions, or the establishment of a marine reserve), then the rate of change for A is expected to increase. We call this a “positive input”. It is formally represented in Figure S1 as the derivative of the growth function for A ( $\partial f(A)$ ) in respect to the variation of  $c$  ( $\partial c$ ). Because parameters in the equations for the growth rate of variables (i.e.  $dA/dt = f(A, B, c, d, e, \dots)$  in which  $c, d, e$  are parameters) define the equilibrium points for the system, changes in parameter values define new equilibrium points with new values for the level of the variables. This parameter variation may influence the abundance of all variables in the model. Loop analysis algorithms predict the direction (increase, decrease, no variation) of change for the level of the variables.

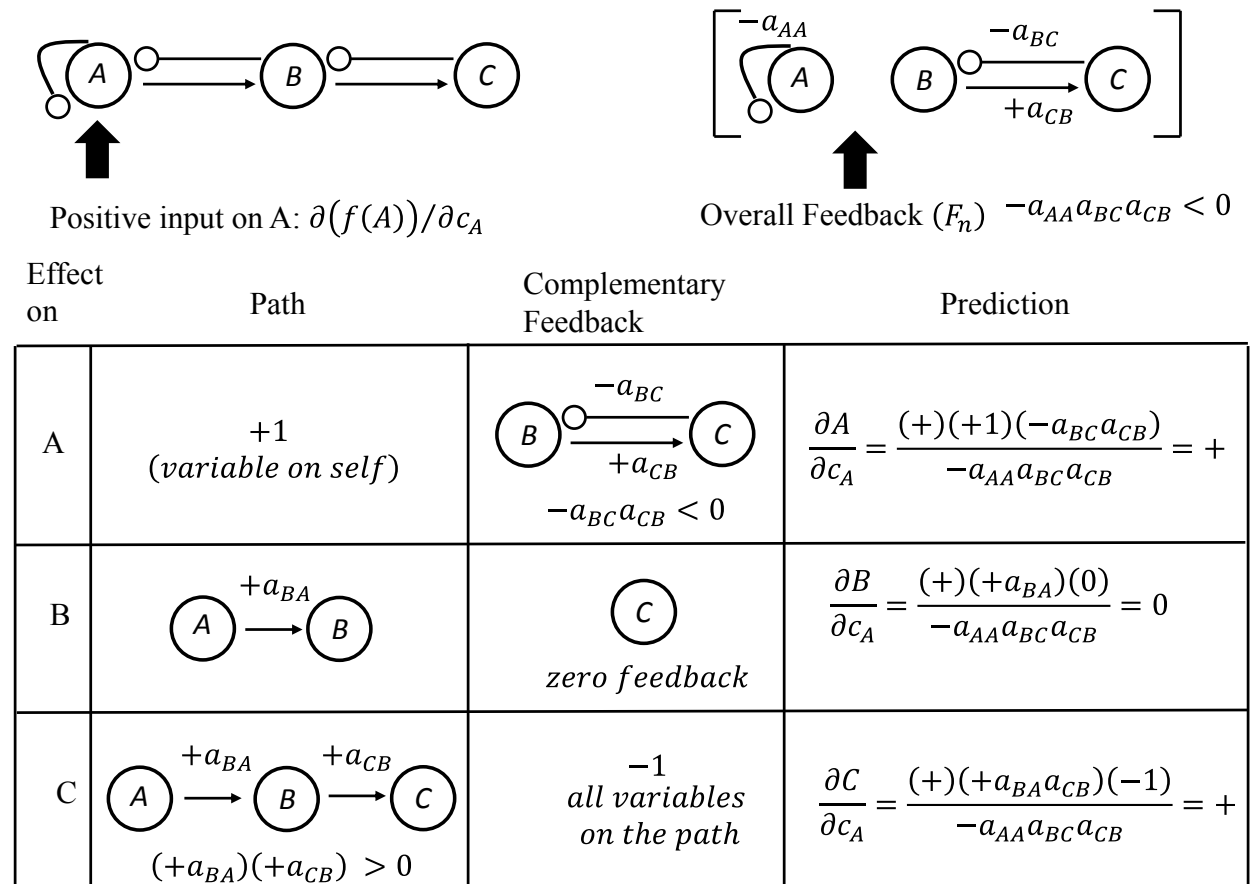
The loop analysis algorithm and its structural elements, with examples of calculations, are visually represented in Figure S1.

The following formula summarizes the elements of the algorithm:

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

Besides the sign of the input, determined by the term  $\left[ \frac{\partial f_i}{\partial c} \right]$ , the loop formula makes use of the concepts of path, circuit, complementary feedback, and overall feedback. These refer to structural elements that can be identified in any graph. Their meaning can be fully understood by referring to the correspondence between matrix algebra and the formalism of loop analysis (see Levins 1975, Puccia and Levins 1985). In the above formula,  $c$  is the changing parameter (e.g., mortality, fecundity, predation rate);  $\left[ \frac{\partial f_i}{\partial c} \right]$  designates if the growth rate of the  $i$  –  $th$  variable is increasing (+) or decreasing (–);  $[p_{ij}^{(k)}]$  is the pathway connecting the variable that undergoes parameter change,  $x_i$ , with that whose equilibrium value is being calculated,  $x_j$ , and that includes ( $k$ ) variables. The last factor of the numerator is the complementary feedback  $[F_{n-k}^{(comp)}]$ , which buffers or reverses the effect of the pathway; it is the feedback formed by the  $(n - k)$  variables that remain in

the system after the ( $k$ ) variables that are on the path are excluded. The term  $[F_n]$  indicates the overall feedback of the system, which is a measure of the inertia of the systems to change. Criteria to identify such elements in the example graph are provided by using the scheme depicted in Figure S1



**Figure S1.** 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 (+).

**Circuits and Feedbacks.** In loop analysis, a pathway that starts at one node and, by following the direction of links, returns to it without crossing intermediate nodes more than once is called a 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 given 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 S1 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 [ $A \rightarrow B$ ] and [ $B \rightarrow C$ ] produce two feedbacks of the second level, and the three variable feedback shown in Figure S1 (overall 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 ( $F_n$ ).** The overall feedback is computed only once and corresponds to the highest possible level of feedback in a system. It can be calculated from single circuits linking all the variables in the system, or as a combination of shorter circuits involving smaller subsets of variables. In the hypothetical chain of three trophic levels depicted in Figure S1, the overall feedback corresponds to a third level of feedback (that is a feedback effect involving all three variables). Because the three variables cannot be connected simultaneously in unique circuits, the overall feedback comprises all the products of disjunct loops that have a combined number of variables equal to 3. That is,  $F_n$  is composed by the self-damping on A (a self-effect link is a loop of length 1) plus the two-node loop [B-C]. 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.

**Path [ $p_{ij}^{(k)}$ ].** A path is a series of links starting at one node and ending on another node, without crossing any variable twice. Suppose a positive input occurs on A (its rate of change increases,  $\left[\frac{\partial f_i}{\partial c}\right] > 0$ ). To predict the new equilibrium of C, the path along which the effect travels is the positive link from A to B and the arrow from B to C. Its sign, given by the product of the signs of the links that form the path, is positive.

**Complementary Feedback ( $F_{n-k}$ ).** The complementary feedback is the feedback that groups all the variables in the complementary subsystem. The complementary subsystem is what remains after the  $(k)$  variables in the path are excluded. In Figure 1, for a positive input on A and effect on B, the complementary subsystem is formed only by C (A and B are on the path). Because C has no self-effect link, in this example there will be a null (0) complementary feedback. A 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, and the complementary feedback is equal to -1. These are two algebraic conveniences that are formally explained in Levins (1975) and Puccia and Levins (1986). Summation in the loop formula considers the fact that two variables can be connected by more than one path.

Using linear algebra, we obtain the same prediction as the graphic algorithm and the net effect (the sum of the direct effect plus all the individual indirect effects) on species  $i$  resulting from an input on species  $j$  is given by the element of the inverse community matrix:



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

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

This means that  $(A_h)$  must have a non-zero determinant and must admit an inverse matrix  $(A_h)^{-1}$  whose eigenvalues have to satisfy the Lyapunov condition of stability.

For simplicity, the vector  $\left( -\frac{\partial \vec{F}}{\partial c_h} \right)$  is considered equal to one because there is no quantitative information about the inputs. A summary table of predictions can be produced from the simulated matrices that satisfy stability conditions. In the overall table, the variables' response is quantified as the percentage of positive signs, negative signs and zero values obtained from the matrices. The sign of the prediction is determined by a set of rules regarding the percentages of cases in which +, - and 0 appear in any given entry of the table, as we explained in the main body of the paper.

## References

- Levins, R. 1975; R. Evolution in Communities Near Equilibrium. M.L. Cody, J. Diamond (Eds.), Ecology and Evolution of Communities, Belknap Press, 16-50.
- Puccia, C., and R. Levins. 1985. *Qualitative Modeling of Complex Systems*. Cambridge, MA: Harvard University Press.

**Table S1. Example of pathways and their signs (Model 1).**

a. Pathways from FS to AS:

FS $\rightarrow$ AS (-)  
FS $\rightarrow$ LS $\rightarrow$ AS (+)  
FS $\rightarrow$ MC $\rightarrow$ MI $\rightarrow$ AE $\rightarrow$ AS (+)  
FS $\rightarrow$ MC $\rightarrow$ MI $\rightarrow$ AE $\rightarrow$ LE $\rightarrow$ LS $\rightarrow$ AS (+)  
FS $\rightarrow$ MC $\rightarrow$ MI $\rightarrow$ LE $\rightarrow$ LS $\rightarrow$ AS (-)  
FS $\rightarrow$ LS $\rightarrow$ LE $\rightarrow$ LC $\rightarrow$ MI $\rightarrow$ AE $\rightarrow$ AS (+)  
FS $\rightarrow$ LS $\rightarrow$ LC $\rightarrow$ MI $\rightarrow$ AE $\rightarrow$ AS (-)  
FS $\rightarrow$ LS $\rightarrow$ LE $\rightarrow$ ME $\rightarrow$ MC $\rightarrow$ MI $\rightarrow$ AE $\rightarrow$ AS (-)

b. Pathways from FS to LS:

FS $\rightarrow$ LS (-)  
FS $\rightarrow$ AS $\rightarrow$ LS (-)  
FS $\rightarrow$ MC $\rightarrow$ MI $\rightarrow$ LE $\rightarrow$ LS (+)  
FS $\rightarrow$ MC $\rightarrow$ MI $\rightarrow$ AE $\rightarrow$ AS $\rightarrow$ LS (+)  
FS $\rightarrow$ MC $\rightarrow$ MI $\rightarrow$ AE $\rightarrow$ LE $\rightarrow$ LS (-)  
FS $\rightarrow$ AS $\rightarrow$ AE $\rightarrow$ LE $\rightarrow$ LS (+)  
FS $\rightarrow$ AS $\rightarrow$ AE $\rightarrow$ ME $\rightarrow$ MC $\rightarrow$ MI $\rightarrow$ LE $\rightarrow$ AS (-)  
FS $\rightarrow$ AS $\rightarrow$ AC $\rightarrow$ MI $\rightarrow$ LE $\rightarrow$ LS (-)  
FS $\rightarrow$ AS $\rightarrow$ AE $\rightarrow$ AC $\rightarrow$ MI $\rightarrow$ LE $\rightarrow$ LS (+)

**Table S2. Simulations' output.** For each of the 5 models (see Figure 2 in the main article), the community matrix, the three matrices reporting the percentage of +, - and 0 obtained in the simulation, and the overall table of predictions are reported.

## Model 1

"Community matrix"

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO
AS	-1	-1	1	1	0	0	1	0	0	0	0	0	0	0
AE	-1	-1	1	0	-1	0	0	-1	0	0	0	0	0	0
AC	0	0	-1	0	0	0	0	0	0	0	0	1	0	0
LS	-1	0	0	-1	-1	1	1	0	0	0	0	0	0	0
LE	0	0	0	-1	-1	1	0	-1	0	0	0	0	0	0
LC	0	0	0	0	0	-1	0	0	0	0	0	1	0	0
FS	-1	0	0	-1	0	0	-1	0	1	0	1	0	0	0
ME	0	0	0	0	0	0	-1	-1	1	0	0	0	0	0
MC	0	0	0	0	0	0	0	-1	-1	0	0	1	0	0
NE	0	0	0	0	0	0	-1	0	0	-1	1	0	0	0
NC	0	0	0	0	0	0	0	0	0	-1	-1	0	1	0
MI	0	-1	0	0	-1	0	0	-1	0	0	0	-1	0	1
NI	0	0	0	0	0	0	0	0	0	-1	0	0	-1	-1
JO	0	0	0	0	0	0	0	0	0	0	0	0	1	-1

Percentage of " + "

	AS	AE	AC	LS	LE	LC	FS	ME
AS	84.92683	14.34146	46.82927	37.31707	65.02439	48.34146	91.56098	28.92683
AE	14.19512	94.04878	76.00000	64.43902	19.70732	26.87805	29.46341	52.34146
AC	52.00000	20.92683	85.31707	44.82927	42.39024	30.92683	78.34146	35.46341
LS	8.48780	80.78049	36.68293	84.82927	16.58537	50.97561	44.97561	57.17073
LE	80.73171	26.00000	52.34146	11.31707	95.90244	73.60976	72.00000	19.31707
LC	52.00000	20.92683	16.78049	44.82927	42.39024	90.09756	78.34146	35.46341
FS	49.65854	55.17073	56.09756	8.68293	76.14634	33.36585	84.00000	21.41463
ME	55.41463	28.78049	26.04878	79.17073	29.56098	53.31707	37.60976	88.63415
MC	49.70732	37.41463	33.02439	19.07317	61.12195	28.87805	85.60976	8.97561
NE	50.34146	44.82927	43.90244	91.31707	23.85366	66.63415	16.00000	78.58537
NC	49.65854	55.17073	56.09756	8.68293	76.14634	33.36585	84.00000	21.41463
MI	52.00000	20.92683	16.78049	44.82927	42.39024	30.92683	78.34146	35.46341
NI	49.65854	55.17073	56.09756	8.68293	76.14634	33.36585	84.00000	21.41463
JO	49.65854	55.17073	56.09756	8.68293	76.14634	33.36585	84.00000	21.41463
	MC	NE	NC	MI	NI	JO		
AS	76.68293	10.24390	78.24390	69.70732	81.85366	45.90244		
AE	35.07317	66.14634	35.56098	47.70732	40.29268	56.34146		
AC	57.75610	15.60976	47.95122	87.80488	87.85366	78.00000		
LS	55.70732	54.87805	48.87805	45.90244	45.85366	46.34146		
LE	32.09756	30.09756	61.70732	59.80488	65.36585	52.73171		
LC	57.75610	15.60976	47.95122	87.80488	87.85366	78.00000		
FS	57.07317	25.21951	82.04878	42.39024	60.29268	29.31707		
ME	83.56098	48.87805	25.46341	77.51220	64.78049	80.00000		
MC	87.46341	16.53659	69.70732	68.63415	77.85366	53.95122		
NE	42.92683	96.92683	85.51220	57.60976	81.21951	24.00000		
NC	57.07317	3.07317	96.92683	42.39024	82.73171	12.78049		
MI	57.75610	15.60976	47.95122	87.80488	87.85366	78.00000		
NI	57.07317	3.07317	14.48780	42.39024	97.90244	4.04878		
JO	57.07317	3.07317	14.48780	42.39024	97.90244	96.78049		

Percentage of " - "

	AS	AE	AC	LS	LE	LC	FS	ME
AS	15.07317	85.65854	53.17073	62.68293	34.97561	51.65854	8.43902	71.07317
AE	85.80488	5.95122	24.00000	35.56098	80.29268	73.12195	70.53659	47.65854
AC	48.00000	79.07317	14.68293	55.17073	57.60976	69.07317	21.65854	64.53659
LS	91.51220	19.21951	63.31707	15.17073	83.41463	49.02439	55.02439	42.82927
LE	19.26829	74.00000	47.65854	88.68293	4.09756	26.39024	28.00000	80.68293
LC	48.00000	79.07317	83.21951	55.17073	57.60976	9.90244	21.65854	64.53659
FS	50.34146	44.82927	43.90244	91.31707	23.85366	66.63415	16.00000	78.58537
ME	44.58537	71.21951	73.95122	20.82927	70.43902	46.68293	62.39024	11.36585
MC	50.29268	62.58537	66.97561	80.92683	38.87805	71.12195	14.39024	91.02439
NE	49.65854	55.17073	56.09756	8.68293	76.14634	33.36585	84.00000	21.41463
NC	50.34146	44.82927	43.90244	91.31707	23.85366	66.63415	16.00000	78.58537
MI	48.00000	79.07317	83.21951	55.17073	57.60976	69.07317	21.65854	64.53659
NI	50.34146	44.82927	43.90244	91.31707	23.85366	66.63415	16.00000	78.58537
JO	50.34146	44.82927	43.90244	91.31707	23.85366	66.63415	16.00000	78.58537

	MC	NE	NC	MI	NI	JO
AS	23.31707	89.75610	21.75610	30.29268	18.14634	54.09756
AE	64.92683	33.85366	64.43902	52.29268	59.70732	43.65854
AC	42.24390	84.39024	52.04878	12.19512	12.14634	22.00000
LS	44.29268	45.12195	51.12195	54.09756	54.14634	53.65854
LE	67.90244	69.90244	38.29268	40.19512	34.63415	47.26829
LC	42.24390	84.39024	52.04878	12.19512	12.14634	22.00000
FS	42.92683	74.78049	17.95122	57.60976	39.70732	70.68293
ME	16.43902	51.12195	74.53659	22.48780	35.21951	20.00000
MC	12.53659	83.46341	30.29268	31.36585	22.14634	46.04878
NE	57.07317	3.07317	14.48780	42.39024	18.78049	76.00000
NC	42.92683	96.92683	3.07317	57.60976	17.26829	87.21951
MI	42.24390	84.39024	52.04878	12.19512	12.14634	22.00000
NI	42.92683	96.92683	85.51220	57.60976	2.09756	95.95122
JO	42.92683	96.92683	85.51220	57.60976	2.09756	3.21951

Percentage of " 0 "

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO
AS	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AE	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AC	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LS	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LE	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LC	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FS	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ME	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MC	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NC	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NI	0	0	0	0	0	0	0	0	0	0	0	0	0	0
JO	0	0	0	0	0	0	0	0	0	0	0	0	0	0

"Table of predictions"

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO
AS	+	-	0*	?-	?+	0*	+	?-	+	-	+	?+	+	0*
AE	-	+	+	?+	-	?-	?-	0*	?-	?+	?-	0*	0*	0*
AC	0*	-	+	0*	0*	?-	+	?-	0*	-	0*	+	+	+
LS	-	+	?-	+	-	0*	0*	0*	0*	0*	0*	0*	0*	0*
LE	+	?-	0*	-	+	?+	?+	-	?-	?-	?+	0*	?+	0*
LC	0*	-	-	0*	0*	+	+	?-	0*	-	0*	+	+	+
FS	0*	0*	0*	-	+	?-	+	-	0*	?-	+	0*	?+	?-
ME	0*	?-	?-	+	?-	0*	?-	+	+	0*	?-	+	?+	+
MC	0*	?-	?-	-	?+	?-	+	-	+	-	?+	?+	+	0*
NE	0*	0*	0*	+	-	?+	-	+	0*	+	+	0*	+	-
NC	0*	0*	0*	-	+	?-	+	-	0*	-	+	0*	+	-
MI	0*	-	-	0*	0*	?-	+	?-	0*	-	0*	+	+	+
NI	0*	0*	0*	-	+	?-	+	-	0*	-	-	0*	+	-



JO 0\* 0\* 0\* - + ?- + - 0\* - - 0\* + +

## Model 2

"Community matrix"

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO
AS	-1	-1	1	1	0	0	1	0	0	0	0	0	0	0
AE	-1	-1	1	0	-1	0	0	-1	0	0	0	0	0	0
AC	0	0	-1	0	0	0	0	0	0	0	0	1	0	0
LS	-1	0	0	-1	-1	1	1	0	0	0	0	0	0	0
LE	0	0	0	-1	-1	1	0	0	0	0	0	0	0	0
LC	0	0	0	0	0	0	-1	0	0	0	0	1	0	0
FS	-1	0	0	-1	0	0	-1	0	1	0	1	0	0	0
ME	0	0	0	0	0	0	-1	-1	1	0	0	0	0	0
MC	0	0	0	0	0	0	0	-1	-1	0	0	1	0	0
NE	0	0	0	0	0	0	-1	0	0	-1	1	0	0	0
NC	0	0	0	0	0	0	0	0	0	-1	-1	0	1	0
MI	0	-1	0	0	-1	0	0	-1	0	0	0	-1	0	1
NI	0	0	0	0	0	0	0	0	0	-1	0	0	-1	-1
JO	0	0	0	0	0	0	0	0	0	0	0	0	1	-1

Percentage of " + "

	AS	AE	AC	LS	LE	LC	FS	ME
AS	86.74699	12.73666	45.78313	40.40448	63.42513	49.65577	91.52324	36.44578
AE	14.54389	94.44923	78.91566	51.46299	25.47332	26.24785	38.72633	28.61446
AC	51.41997	21.60069	84.50947	44.14802	39.02754	30.63683	80.76592	30.37866
LS	6.49742	86.61790	44.62134	80.37866	18.76076	49.91394	51.50602	33.73494
LE	90.74871	7.91738	38.72633	20.09466	94.79346	79.86231	64.58692	52.15146
LC	51.41997	21.60069	16.56627	44.14802	39.02754	92.03959	80.76592	30.37866
FS	53.91566	46.55766	48.92427	7.96041	79.25990	35.28399	84.50947	32.44406
ME	48.36489	36.53184	30.59380	83.26162	24.35456	50.30120	34.63855	89.37177
MC	54.08778	31.84165	31.84165	17.34079	63.51119	31.45439	85.92943	10.71429
NE	46.08434	53.44234	51.07573	92.03959	20.74010	64.71601	15.49053	67.55594
NC	53.91566	46.55766	48.92427	7.96041	79.25990	35.28399	84.50947	32.44406
MI	51.41997	21.60069	16.56627	44.14802	39.02754	30.63683	80.76592	30.37866
NI	53.91566	46.55766	48.92427	7.96041	79.25990	35.28399	84.50947	32.44406
JO	53.91566	46.55766	48.92427	7.96041	79.25990	35.28399	84.50947	32.44406

	MC	NE	NC	MI	NI	JO
AS	88.72633	9.29432	75.21515	73.10671	84.59552	50.60241
AE	16.17900	61.83305	45.95525	40.83477	39.19966	44.79346
AC	55.03442	13.94148	48.75215	89.54389	88.81239	78.14114
LS	34.81067	26.62478	58.39071	36.61790	41.82444	35.92943
LE	64.28571	29.30293	43.11532	80.24957	76.89329	73.92427
LC	55.03442	13.94148	48.75215	89.54389	88.81239	78.14114
FS	75.38726	22.03098	78.14114	51.80723	66.69535	36.44578
ME	81.11015	53.82960	24.82788	72.54733	59.98279	77.45267
MC	92.81411	14.97418	66.56627	73.02065	80.98107	57.18589
NE	24.61274	97.03098	86.53184	48.19277	79.43201	21.90189
NC	75.38726	2.96902	95.05164	51.80723	86.35972	17.16867
MI	55.03442	13.94148	48.75215	89.54389	88.81239	78.14114
NI	75.38726	2.96902	13.46816	51.80723	98.45095	5.59380
JO	75.38726	2.96902	13.46816	51.80723	98.45095	96.68675

Percentage of " - "

	AS	AE	AC	LS	LE	LC	FS	ME
AS	13.25301	87.26334	54.21687	59.59552	36.57487	50.34423	8.47676	63.55422
AE	85.45611	5.55077	21.08434	48.53701	74.52668	73.75215	61.27367	71.38554
AC	48.58003	78.39931	15.49053	55.85198	60.97246	69.36317	19.23408	69.62134
LS	93.50258	13.38210	55.37866	19.62134	81.23924	50.08606	48.49398	66.26506
LE	9.25129	92.08262	61.27367	79.90534	5.20654	20.13769	35.41308	47.84854
LC	48.58003	78.39931	83.43373	55.85198	60.97246	7.96041	19.23408	69.62134
FS	46.08434	53.44234	51.07573	92.03959	20.74010	64.71601	15.49053	67.55594
ME	51.63511	63.46816	69.40620	16.73838	75.64544	49.69880	65.36145	10.62823
MC	45.91222	68.15835	68.15835	82.65921	36.48881	68.54561	14.07057	89.28571
NE	53.91566	46.55766	48.92427	7.96041	79.25990	35.28399	84.50947	32.44406
NC	46.08434	53.44234	51.07573	92.03959	20.74010	64.71601	15.49053	67.55594
MI	48.58003	78.39931	83.43373	55.85198	60.97246	69.36317	19.23408	69.62134

NI	46.08434	53.44234	51.07573	92.03959	20.74010	64.71601	15.49053	67.55594
JO	46.08434	53.44234	51.07573	92.03959	20.74010	64.71601	15.49053	67.55594
	MC	NE	NC	MI	NI	JO		
AS	11.27367	90.70568	24.78485	26.89329	15.40448	49.39759		
AE	83.82100	38.16695	54.04475	59.16523	60.80034	55.20654		
AC	44.96558	86.05852	51.24785	10.45611	11.18761	21.85886		
LS	65.18933	47.37522	41.60929	63.38210	58.17556	64.07057		
LE	35.71429	70.69707	56.88468	19.75043	23.10671	26.07573		
LC	44.96558	86.05852	51.24785	10.45611	11.18761	21.85886		
FS	24.61274	77.96902	21.85886	48.19277	33.30465	63.55422		
ME	18.88985	46.17040	75.17212	27.45267	40.01721	22.54733		
MC	7.18589	85.02582	33.43373	26.97935	19.01893	42.81411		
NE	75.38726	2.96902	13.46816	51.80723	20.56799	78.09811		
NC	24.61274	97.03098	4.94836	48.19277	13.64028	82.83133		
MI	44.96558	86.05852	51.24785	10.45611	11.18761	21.85886		
NI	24.61274	97.03098	86.53184	48.19277	1.54905	94.40620		
JO	24.61274	97.03098	86.53184	48.19277	1.54905	3.31325		

Percentage of " 0 "

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO
AS	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AE	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AC	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LS	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LE	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LC	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FS	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ME	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MC	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NC	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NI	0	0	0	0	0	0	0	0	0	0	0	0	0	0
JO	0	0	0	0	0	0	0	0	0	0	0	0	0	0

"Table of predictions"

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO
AS	+	-	0*	0*	?+	0*	+	?-	+	-	+	?+	+	0*
AE	-	+	+	0*	?-	?-	?-	-	?	+	0*	0*	?-	0*
AC	0*	-	+	0*	?-	?-	+	?-	0*	-	0*	+	+	+
LS	-	+	0*	+	-	0*	0*	?-	?-	0*	0*	?-	0*	?-
LE	+	-	?-	-	+	+	?+	0*	?+	?-	0*	+	+	?+
LC	0*	-	-	0*	?-	+	+	?-	0*	-	0*	+	+	+
FS	0*	0*	0*	-	+	?-	+	?-	+	-	+	0*	?+	?-
ME	0*	?-	?-	+	-	0*	?-	+	+	0*	-	?+	0*	+
MC	0*	?-	?-	-	?+	?-	+	-	+	-	?+	?+	+	0*
NE	0*	0*	0*	+	-	?+	-	?+	-	+	+	0*	+	-
NC	0*	0*	0*	-	+	?-	+	?-	+	-	+	0*	+	-
MI	0*	-	-	0*	?-	?-	+	?-	0*	-	0*	+	+	+
NI	0*	0*	0*	-	+	?-	+	?-	+	-	-	0*	+	-
JO	0*	0*	0*	-	+	?-	+	?-	+	-	-	0*	+	+

## Model 3

"Community matrix"

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO
AS	-1	-1	1	1	0	0	1	0	0	0	0	0	0	0
AE	-1	-1	1	0	0	0	0	-1	0	0	0	0	0	0
AC	0	0	-1	0	0	0	0	0	0	0	0	1	0	0
LS	-1	0	0	-1	-1	1	1	0	0	0	0	0	0	0
LE	0	0	0	-1	-1	1	0	-1	0	0	0	0	0	0
LC	0	0	0	0	0	-1	0	0	0	0	0	1	0	0
FS	-1	0	0	-1	0	0	-1	0	1	0	1	0	0	0
ME	0	0	0	0	0	0	-1	-1	1	0	0	0	0	0
MC	0	0	0	0	0	0	0	-1	-1	0	0	1	0	0
NE	0	0	0	0	0	0	-1	0	0	-1	1	0	0	0
NC	0	0	0	0	0	0	0	0	0	-1	-1	0	1	0
MI	0	-1	0	0	-1	0	0	-1	0	0	0	-1	0	1

NI	0	0	0	0	0	0	0	0	0	0	-1	0	0	-1	-1
JO	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-1

Percentage of " + "

	AS	AE	AC	LS	LE	LC	FS	ME
AS	83.35221	15.85504	44.69611	50.77388	38.69385	33.03133	90.48698	43.18611
AE	22.31031	93.01623	85.69271	35.03209	54.51114	41.63835	37.63684	27.89732
AC	42.61986	22.95206	87.31597	62.77841	15.66629	18.27105	72.78218	50.32088
LS	6.34202	83.88071	41.33635	79.01095	30.46433	62.24991	48.24462	42.24236
LE	86.74972	18.27105	45.86636	14.60929	92.63873	73.68818	73.27293	26.50057
LC	42.61986	22.95206	14.94904	62.77841	15.66629	88.48622	72.78218	50.32088
FS	56.02114	47.94262	53.86938	4.75651	85.99471	34.76784	87.91997	17.74254
ME	41.71385	38.12760	28.31257	89.99622	8.19177	43.79011	31.67233	91.92148
MC	49.94337	33.63533	31.33258	22.65006	54.13364	21.70630	87.46697	11.74028
NE	43.97886	52.05738	46.13062	95.24349	14.00529	65.23216	12.08003	82.25746
NC	56.02114	47.94262	53.86938	4.75651	85.99471	34.76784	87.91997	17.74254
MI	42.61986	22.95206	14.94904	62.77841	15.66629	18.27105	72.78218	50.32088
NI	56.02114	47.90487	53.83163	4.75651	85.95696	34.76784	87.88222	17.74254
JO	56.02114	47.90487	53.83163	4.75651	85.99471	34.76784	87.91997	17.74254
	MC	NE	NC	MI	NI	JO		
AS	87.31597	11.58928	76.67044	67.64817	81.23820	44.84711		
AE	16.53454	57.07814	35.18309	58.36165	51.03813	62.70291		
AC	68.10117	19.47905	41.37410	91.88373	87.35372	82.25746		
LS	42.77086	50.28313	49.30162	49.75462	50.13213	49.11287		
LE	43.22386	27.67082	61.57040	64.85466	68.89392	53.11438		
LC	68.10117	19.47905	41.37410	91.88373	87.35372	82.25746		
FS	58.73915	20.27180	84.59796	46.28162	65.87391	30.57758		
ME	81.27595	54.92639	20.00755	76.06644	59.00340	81.46470		
MC	89.31672	13.74103	66.81767	74.44319	82.29521	58.02190		
NE	41.26085	97.31974	82.97471	53.71838	79.35070	25.36806		
NC	58.73915	2.68026	96.97999	46.28162	85.57946	13.70328		
MI	68.10117	19.47905	41.37410	91.88373	87.35372	82.25746		
NI	58.70140	2.68026	17.02529	46.24387	97.99924	3.66176		
JO	58.70140	2.68026	17.02529	46.28162	97.99924	95.92299		

Percentage of " - "

	AS	AE	AC	LS	LE	LC	FS	ME
AS	16.64779	84.14496	55.30389	49.22612	61.30615	66.96867	9.51302	56.81389
AE	77.68969	6.98377	14.30729	64.96791	45.48886	58.36165	62.36316	72.10268
AC	57.38014	77.04794	12.68403	37.22159	84.33371	81.72895	27.21782	49.67912
LS	93.65798	16.11929	58.66365	20.98905	69.53567	37.75009	51.75538	57.75764
LE	13.25028	81.72895	54.13364	85.39071	7.36127	26.31182	26.72707	73.49943
LC	57.38014	77.04794	85.05096	37.22159	84.33371	11.51378	27.21782	49.67912
FS	43.97886	52.05738	46.13062	95.24349	14.00529	65.23216	12.08003	82.25746
ME	58.28615	61.87240	71.68743	10.00378	91.80823	56.20989	68.32767	8.07852
MC	50.05663	66.36467	68.66742	77.34994	45.86636	78.29370	12.53303	88.25972
NE	56.02114	47.94262	53.86938	4.75651	85.99471	34.76784	87.91997	17.74254
NC	43.97886	52.05738	46.13062	95.24349	14.00529	65.23216	12.08003	82.25746
MI	57.38014	77.04794	85.05096	37.22159	84.33371	81.72895	27.21782	49.67912
NI	43.94111	52.05738	46.09287	95.20574	13.96753	65.19441	12.08003	82.21971
JO	43.97886	52.05738	46.09287	95.24349	14.00529	65.19441	12.08003	82.21971
	MC	NE	NC	MI	NI	JO		
AS	12.68403	88.41072	23.32956	32.35183	18.76180	55.15289		
AE	83.46546	42.92186	64.81691	41.63835	48.96187	37.29709		
AC	31.89883	80.52095	58.62590	8.11627	12.64628	17.74254		
LS	57.22914	49.71687	50.69838	50.24538	49.86787	50.88713		
LE	56.77614	72.32918	38.42960	35.14534	31.10608	46.88562		
LC	31.89883	80.52095	58.62590	8.11627	12.64628	17.74254		
FS	41.26085	79.72820	15.40204	53.71838	34.12609	69.42242		
ME	18.72405	45.07361	79.99245	23.93356	40.99660	18.53530		
MC	10.68328	86.25897	33.18233	25.55681	17.70479	41.97810		
NE	58.70140	2.68026	17.02529	46.28162	20.64930	74.63194		
NC	41.26085	97.31974	3.02001	53.71838	14.42054	86.29672		
MI	31.89883	80.52095	58.62590	8.11627	12.64628	17.74254		
NI	41.22310	97.31974	82.97471	53.71838	2.00076	96.33824		
JO	41.26085	97.31974	82.97471	53.71838	2.00076	4.07701		

Percentage of " 0 "

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC
AS	0.00000	0.00000	0.0000	0.00000	0.0000	0.00000	0.00000	0.00000	0.00000	0	0
AE	0.00000	0.00000	0.0000	0.00000	0.0000	0.00000	0.00000	0.00000	0.00000	0	0
AC	0.00000	0.00000	0.0000	0.00000	0.0000	0.00000	0.00000	0.00000	0.00000	0	0
LS	0.00000	0.00000	0.0000	0.00000	0.0000	0.00000	0.00000	0.00000	0.00000	0	0
LE	0.00000	0.00000	0.0000	0.00000	0.0000	0.00000	0.00000	0.00000	0.00000	0	0
LC	0.00000	0.00000	0.0000	0.00000	0.0000	0.00000	0.00000	0.00000	0.00000	0	0
FS	0.00000	0.00000	0.0000	0.00000	0.0000	0.00000	0.00000	0.00000	0.00000	0	0
ME	0.00000	0.00000	0.0000	0.00000	0.0000	0.00000	0.00000	0.00000	0.00000	0	0
MC	0.00000	0.00000	0.0000	0.00000	0.0000	0.00000	0.00000	0.00000	0.00000	0	0
NE	0.00000	0.00000	0.0000	0.00000	0.0000	0.00000	0.00000	0.00000	0.03775	0	0
NC	0.00000	0.00000	0.0000	0.00000	0.0000	0.00000	0.00000	0.00000	0.00000	0	0
MI	0.00000	0.00000	0.0000	0.00000	0.0000	0.00000	0.00000	0.00000	0.00000	0	0
NI	0.03775	0.03775	0.0755	0.03775	0.0755	0.03775	0.03775	0.03775	0.07550	0	0
JO	0.00000	0.03775	0.0755	0.00000	0.0000	0.03775	0.00000	0.03775	0.03775	0	0

MI NI JO

AS	0.00000	0	0
AE	0.00000	0	0
AC	0.00000	0	0
LS	0.00000	0	0
LE	0.00000	0	0
LC	0.00000	0	0
FS	0.00000	0	0
ME	0.00000	0	0
MC	0.00000	0	0
NE	0.00000	0	0
NC	0.00000	0	0
MI	0.00000	0	0
NI	0.03775	0	0
JO	0.00000	0	0

"Table of predictions"

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO
AS	+	-	0*	0*	?-	?-	+	0*	+	-	+	?+	+	0*
AE	-	+	+	?-	0*	0*	?-	?-	-	0*	?-	0*	0*	?+
AC	0*	-	+	?+	-	-	?+	0*	?+	-	0*	+	+	+
LS	-	+	0*	+	?-	?+	0*	0*	0*	0*	0*	0*	0*	0*
LE	+	-	0*	-	+	?+	?+	?-	0*	?-	?+	?+	?+	0*
LC	0*	-	-	?+	-	+	?+	0*	?+	-	0*	+	+	+
FS	0*	0*	0*	-	+	?-	+	-	0*	-	+	0*	?+	?-
ME	0*	?-	?-	+	-	0*	?-	+	+	0*	-	+	0*	+
MC	0*	?-	?-	-	0*	-	+	-	+	-	?+	?+	+	0*
NE	0*	0*	0*	+	-	?+	-	+	0*	+	+	0*	+	?-
NC	0*	0*	0*	-	+	?-	+	-	0*	-	+	0*	+	-
MI	0*	-	-	?+	-	-	?+	0*	?+	-	0*	+	+	+
NI	0*	0*	0*	-	+	?-	+	-	0*	-	-	0*	+	-
JO	0*	0*	0*	-	+	?-	+	-	0*	-	-	0*	+	+

## Model 4

"Community matrix"

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO
AS	-1	-1	1	1	0	0	1	0	0	0	0	0	0	0
AE	-1	-1	1	0	0	0	0	-1	0	0	0	0	0	0
AC	0	0	-1	0	0	0	0	0	0	0	0	1	0	0
LS	-1	0	0	-1	-1	1	1	0	0	0	0	0	0	0
LE	0	0	0	-1	-1	1	0	0	0	0	0	0	0	0
LC	0	0	0	0	0	-1	0	0	0	0	0	1	0	0
FS	-1	0	0	-1	0	0	-1	0	1	0	1	0	0	0
ME	0	0	0	0	0	0	-1	-1	1	0	0	0	0	0
MC	0	0	0	0	0	0	0	-1	-1	0	0	1	0	0
NE	0	0	0	0	0	0	-1	0	0	-1	1	0	0	0
NC	0	0	0	0	0	0	0	0	0	-1	-1	0	1	0
MI	0	-1	0	0	-1	0	0	-1	0	0	0	-1	0	1
NI	0	0	0	0	0	0	0	0	0	-1	0	0	-1	-1

JO 0 0 0 0 0 0 0 0 0 0 0 0 0 1 -1

Percentage of " + "

	AS	AE	AC	LS	LE	LC	FS	ME
AS	87.14910	10.85465	44.38553	48.28447	38.67748	33.15658	94.91578	37.89769
AE	22.83219	93.32502	85.21522	32.03369	58.82720	42.63880	37.61697	22.70742
AC	43.38740	22.08359	88.55271	53.33749	17.52963	15.62695	83.37492	27.97879
LS	5.36494	87.52339	42.45165	76.07611	33.00062	63.03805	49.25140	28.38428
LE	92.70119	5.80162	36.11978	25.04679	89.83157	77.23019	68.27823	54.99064
LC	43.38740	22.08359	16.03244	53.33749	17.52963	91.70306	83.37492	27.97879
FS	58.67124	40.04991	47.50468	5.05303	84.74735	31.87773	88.67748	31.72177
ME	38.39676	41.89021	29.94386	89.55084	8.35933	42.23331	33.21896	89.23893
MC	52.74485	29.66313	28.13475	19.96257	54.49158	20.24329	91.26638	8.04741
NE	41.32876	59.95009	52.49532	94.94697	15.25265	68.12227	11.32252	68.27823
NC	58.67124	40.04991	47.50468	5.05303	84.74735	31.87773	88.67748	31.72177
MI	43.38740	22.08359	16.03244	53.33749	17.52963	15.62695	83.37492	27.97879
NI	58.67124	40.04991	47.50468	5.05303	84.74735	31.84654	88.67748	31.72177
JO	58.64005	40.04991	47.50468	5.05303	84.74735	31.81535	88.67748	31.72177
	MC	NE	NC	MI	NI	JO		
AS	92.91953	8.14099	82.84467	71.36619	84.31067	43.73051		
AE	12.60137	57.42358	35.52714	56.70618	50.56145	61.10418		
AC	56.76856	12.50780	52.24579	92.85714	91.11042	79.75671		
LS	29.94386	52.46413	51.99626	42.57642	45.72676	42.88833		
LE	70.61759	25.67062	47.84779	82.09607	78.54024	73.08172		
LC	56.76856	12.50780	52.24579	92.85714	91.11042	79.75671		
FS	78.85215	16.99938	81.09794	56.92452	72.36432	36.36931		
ME	78.32190	55.36494	23.83032	73.58079	59.07673	79.91266		
MC	94.72863	10.66750	70.96070	78.97692	86.18216	59.01435		
NE	21.14785	98.44042	84.77854	43.07548	76.88709	19.83780		
NC	78.85215	1.55958	96.10106	56.92452	89.70680	17.40487		
MI	56.76856	12.50780	52.24579	92.85714	91.11042	79.75671		
NI	78.85215	1.55958	15.22146	56.89333	99.25140	4.83468		
JO	78.85215	1.55958	15.22146	56.86213	99.25140	97.31753		

Percentage of " - "

	AS	AE	AC	LS	LE	LC	FS	ME
AS	12.85090	89.14535	55.61447	51.71553	61.32252	66.84342	5.08422	62.10231
AE	77.16781	6.67498	14.78478	67.96631	41.17280	57.36120	62.38303	77.29258
AC	56.61260	77.91641	11.44729	46.66251	82.47037	84.37305	16.62508	72.02121
LS	94.63506	12.47661	57.54835	23.92389	66.99938	36.96195	50.74860	71.61572
LE	7.29881	94.19838	63.88022	74.95321	10.16843	22.76981	31.72177	45.00936
LC	56.61260	77.91641	83.96756	46.66251	82.47037	8.29694	16.62508	72.02121
FS	41.32876	59.95009	52.49532	94.94697	15.25265	68.12227	11.32252	68.27823
ME	61.60324	58.10979	70.05614	10.44916	91.64067	57.76669	66.78104	10.76107
MC	47.25515	70.33687	71.86525	80.03743	45.50842	79.75671	8.73362	91.95259
NE	58.67124	40.04991	47.50468	5.05303	84.74735	31.87773	88.67748	31.72177
NC	41.32876	59.95009	52.49532	94.94697	15.25265	68.12227	11.32252	68.27823
MI	56.61260	77.91641	83.96756	46.66251	82.47037	84.37305	16.62508	72.02121
NI	41.32876	59.95009	52.46413	94.94697	15.25265	68.12227	11.32252	68.24704
JO	41.29757	59.91890	52.49532	94.94697	15.25265	68.12227	11.32252	68.24704
	MC	NE	NC	MI	NI	JO		
AS	7.08047	91.85901	17.15533	28.63381	15.68933	56.26949		
AE	87.39863	42.57642	64.44167	43.29382	49.43855	38.89582		
AC	43.23144	87.49220	47.75421	7.14286	8.88958	20.24329		
LS	70.05614	47.53587	48.00374	57.42358	54.27324	57.11167		
LE	29.38241	74.32938	52.15221	17.90393	21.45976	26.91828		
LC	43.23144	87.49220	47.75421	7.14286	8.88958	20.24329		
FS	21.14785	83.00062	18.90206	43.07548	27.63568	63.63069		
ME	21.67810	44.63506	76.16968	26.41921	40.92327	20.08734		
MC	5.27137	89.33250	29.03930	21.02308	13.81784	40.98565		
NE	78.85215	1.55958	15.22146	56.92452	23.11291	80.16220		
NC	21.14785	98.44042	3.89894	43.07548	10.29320	82.59513		
MI	43.23144	87.49220	47.75421	7.14286	8.88958	20.24329		
NI	21.14785	98.44042	84.77854	43.07548	0.74860	95.16532		
JO	21.14785	98.44042	84.77854	43.07548	0.74860	2.68247		



Percentage of " 0 "															
	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO	
AS	0.00000	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0	0.00000	0.00000	0	0	
AE	0.00000	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0	0.03119	0.00000	0	0	
AC	0.00000	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0	0.00000	0.00000	0	0	
LS	0.00000	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0	0.00000	0.00000	0	0	
LE	0.00000	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0	0.00000	0.00000	0	0	
LC	0.00000	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0	0.00000	0.00000	0	0	
FS	0.00000	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0	0.00000	0.00000	0	0	
ME	0.00000	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0	0.00000	0.00000	0	0	
MC	0.00000	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0	0.00000	0.00000	0	0	
NE	0.00000	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0	0.00000	0.00000	0	0	
NC	0.00000	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0	0.00000	0.00000	0	0	
MI	0.00000	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0	0.00000	0.00000	0	0	
NI	0.00000	0.00000	0.03119	0	0	0.03119	0	0.03119	0	0	0.00000	0.03119	0	0	
JO	0.06238	0.03119	0.00000	0	0	0.06238	0	0.03119	0	0	0.00000	0.06238	0	0	

# "Table of predictions"

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO	
AS	+	-	0*	0*	?-	?-	+	?-	+	-	+	?+	+	0*	
AE	-	+	+	?-	0*	0*	?-	-	-	0*	?-	0*	0*	?+	
AC	0*	-	+	0*	-	-	+	?-	0*	-	0*	+	+	+	
LS	-	+	0*	+	?-	?+	0*	?-	?-	0*	0*	0*	0*	0*	
LE	+	-	?-	?-	+	+	?+	0*	?+	?-	0*	+	+	?+	
LC	0*	-	-	0*	-	+	+	?-	0*	-	0*	+	+	+	
FS	0*	0*	0*	-	+	?-	+	?-	+	-	+	0*	?+	?-	
ME	?-	0*	?-	+	-	0*	?-	+	+	0*	-	?+	0*	+	
MC	0*	?-	?-	-	0*	-	+	-	+	-	?+	+	+	0*	
NE	0*	0*	0*	+	-	?+	-	?+	-	+	+	0*	+	-	
NC	0*	0*	0*	-	+	?-	+	?-	+	-	+	0*	+	-	
MI	0*	-	-	0*	-	-	+	?-	0*	-	0*	+	+	+	
NI	0*	0*	0*	-	+	?-	+	?-	+	-	-	0*	+	-	
JO	0*	0*	0*	-	+	?-	+	?-	+	-	-	0*	+	+	

## Model 5

### "Community matrix"

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO	
AS	-1	-1	1	1	0	0	1	0	0	0	0	0	0	0	
AE	-1	-1	1	0	0	0	0	0	0	0	0	0	0	0	
AC	0	0	-1	0	0	0	0	0	0	0	0	1	0	0	
LS	-1	0	0	-1	-1	1	1	0	0	0	0	0	0	0	
LE	0	0	0	-1	-1	1	0	-1	0	0	0	0	0	0	
LC	0	0	0	0	0	-1	0	0	0	0	0	1	0	0	
FS	-1	0	0	-1	0	0	-1	0	1	0	1	0	0	0	
ME	0	0	0	0	0	0	-1	-1	1	0	0	0	0	0	
MC	0	0	0	0	0	0	0	-1	-1	0	0	1	0	0	
NE	0	0	0	0	0	0	-1	0	0	-1	1	0	0	0	
NC	0	0	0	0	0	0	0	0	0	-1	-1	0	1	0	
MI	0	-1	0	0	-1	0	0	-1	0	0	0	-1	0	1	
NI	0	0	0	0	0	0	0	0	0	-1	0	0	-1	-1	
JO	0	0	0	0	0	0	0	0	0	0	0	0	1	-1	

### Percentage of " + "

	AS	AE	AC	LS	LE	LC	FS	ME	
AS	83.62847	16.43836	48.94754	41.79753	48.17908	34.38022	93.55162	20.84865	
AE	12.22853	94.82125	82.15837	59.17140	30.83862	38.42299	20.11360	65.08520	
AC	45.53959	23.15403	89.54227	51.55363	22.45239	15.60307	79.88640	30.80521	
LS	7.51754	81.22285	35.51620	86.83595	21.11594	60.37421	43.76879	66.32142	
LE	81.25626	23.98931	52.75643	8.72035	95.75677	72.26863	74.07284	9.48881	
LC	45.53959	23.15403	16.70565	51.55363	22.45239	88.00535	79.88640	30.80521	
FS	51.62045	52.32208	55.89709	4.64417	86.46843	35.21550	85.16539	14.46709	
ME	47.21016	33.37788	24.15636	88.60675	9.55563	41.59706	36.98630	91.91447	
MC	46.87604	36.25125	33.41129	20.14701	56.99967	21.48346	87.37053	6.88273	
NE	48.37955	47.67792	44.10291	95.35583	13.53157	64.78450	14.83461	85.53291	
NC	51.62045	52.32208	55.89709	4.64417	86.46843	35.21550	85.16539	14.46709	
MI	45.53959	23.15403	16.70565	51.55363	22.45239	15.60307	79.88640	30.80521	

NI	51.62045	52.28867	55.89709	4.64417	86.46843	35.21550	85.16539	14.46709
JO	51.58704	52.28867	55.89709	4.64417	86.43502	35.21550	85.16539	14.40027
	MC	NE	NC	MI	NI	JO		
AS	79.31841	10.12362	84.29669	62.11159	79.45205	37.72135		
AE	27.46408	66.72235	15.03508	72.33545	51.58704	81.72402		
AC	58.46976	15.20214	49.44871	89.97661	88.74039	77.88172		
LS	61.37655	52.72302	41.76412	57.50084	51.98797	58.43635		
LE	24.65753	29.00100	67.15670	56.53191	65.18543	45.94053		
LC	58.46976	15.20214	49.44871	89.97661	88.74039	77.88172		
FS	53.62513	21.65052	83.02706	44.97160	63.84898	28.76712		
ME	88.43969	52.15503	23.35449	77.74808	63.14734	82.05814		
MC	87.43735	13.83228	70.49783	73.13732	81.52355	54.66088		
NE	46.37487	97.19345	82.75977	55.02840	79.38523	25.42599		
NC	53.62513	2.80655	96.55864	44.97160	85.16539	12.49582		
MI	58.46976	15.20214	49.44871	89.97661	88.74039	77.88172		
NI	53.62513	2.80655	17.24023	44.93819	98.26261	3.64183		
JO	53.62513	2.80655	17.24023	44.90478	98.26261	95.95723		

Percentage of " - "

	AS	AE	AC	LS	LE	LC	FS	ME
AS	16.37153	83.56164	51.05246	58.20247	51.82092	65.61978	6.44838	79.15135
AE	87.77147	5.17875	17.84163	40.82860	69.16138	61.57701	79.88640	34.91480
AC	54.46041	76.84597	10.45773	48.44637	77.54761	84.39693	20.11360	69.19479
LS	92.48246	18.77715	64.48380	13.16405	78.88406	39.62579	56.23121	33.67858
LE	18.74374	76.01069	47.24357	91.27965	4.24323	27.73137	25.92716	90.51119
LC	54.46041	76.84597	83.29435	48.44637	77.54761	11.99465	20.11360	69.19479
FS	48.37955	47.67792	44.10291	95.35583	13.53157	64.78450	14.83461	85.53291
ME	52.78984	66.62212	75.84364	11.39325	90.44437	58.40294	63.01370	8.08553
MC	53.12396	63.74875	66.58871	79.85299	43.00033	78.51654	12.62947	93.11727
NE	51.62045	52.32208	55.89709	4.64417	86.46843	35.21550	85.16539	14.46709
NC	48.37955	47.67792	44.10291	95.35583	13.53157	64.78450	14.83461	85.53291
MI	54.46041	76.84597	83.29435	48.44637	77.54761	84.39693	20.11360	69.19479
NI	48.37955	47.67792	44.03608	95.35583	13.53157	64.78450	14.83461	85.53291
JO	48.37955	47.64450	44.03608	95.28901	13.53157	64.75109	14.83461	85.53291
	MC	NE	NC	MI	NI	JO		
AS	20.68159	89.87638	15.70331	37.88841	20.54795	62.27865		
AE	72.53592	33.27765	84.96492	27.66455	48.41296	18.27598		
AC	41.53024	84.79786	50.55129	9.98998	11.25961	22.11828		
LS	38.62345	47.27698	58.23588	42.49916	48.01203	41.56365		
LE	75.34247	70.99900	32.84330	43.46809	34.81457	54.05947		
LC	41.53024	84.79786	50.55129	9.98998	11.25961	22.11828		
FS	46.37487	78.34948	16.97294	55.02840	36.15102	71.23288		
ME	11.56031	47.84497	76.64551	22.25192	36.85266	17.94186		
MC	12.56265	86.16772	29.50217	26.86268	18.47645	45.33912		
NE	53.62513	2.80655	17.24023	44.97160	20.61477	74.57401		
NC	46.37487	97.19345	3.44136	55.02840	14.83461	87.50418		
MI	41.53024	84.79786	50.55129	9.98998	11.25961	22.11828		
NI	46.37487	97.19345	82.75977	55.02840	1.73739	96.35817		
JO	46.34146	97.19345	82.75977	54.99499	1.73739	4.04277		

Percentage of " 0 "

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC
AS	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
AE	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
AC	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
LS	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
LE	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
LC	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
FS	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
ME	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
MC	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
NE	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
NC	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
MI	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
NI	0.00000	0.03341	0.06682	0.00000	0.00000	0.00000	0	0.00000	0.00000	0	0
JO	0.03341	0.06682	0.06682	0.06682	0.03341	0.03341	0	0.06682	0.03341	0	0
	MI	NI	JO								
AS	0.00000	0	0								

```

AE 0.00000 0 0
AC 0.03341 0 0
LS 0.00000 0 0
LE 0.00000 0 0
LC 0.03341 0 0
FS 0.00000 0 0
ME 0.00000 0 0
MC 0.00000 0 0
NE 0.00000 0 0
NC 0.00000 0 0
MI 0.03341 0 0
NI 0.03341 0 0
JO 0.10023 0 0

```

"Table of predictions"

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO
AS	+	-	0*	0*	0*	?-	+	-	+	-	+	?+	+	?-
AE	-	+	+	0*	?-	?-	-	?+	?-	?+	-	?+	0*	+
AC	0*	-	+	0*	-	-	+	?-	0*	-	0*	+	+	+
LS	-	+	?-	+	-	?+	0*	?+	?+	0*	0*	0*	0*	0*
LE	+	-	0*	-	+	?+	?+	-	-	?-	?+	0*	?+	0*
LC	0*	-	-	0*	-	+	+	?-	0*	-	0*	+	+	+
FS	0*	0*	0*	-	+	?-	+	-	0*	-	+	0*	?+	?-
ME	0*	?-	-	+	-	0*	?-	+	+	0*	-	+	?+	+
MC	0*	?-	?-	-	0*	-	+	-	+	-	?+	?+	+	0*
NE	0*	0*	0*	+	-	?+	-	+	0*	+	+	0*	+	?-
NC	0*	0*	0*	-	+	?-	+	-	0*	-	+	0*	+	-
MI	0*	-	-	0*	-	-	+	?-	0*	-	0*	+	+	+
NI	0*	0*	0*	-	+	?-	+	-	0*	-	-	0*	+	-
JO	0*	0*	0*	-	+	?-	+	-	0*	-	-	0*	+	+

**Table S3. Sensitivity Analyses.** Number of cases in which each prediction matrix differs from all other matrices in a series of pairwise comparisons.

a. Numbers based on tendencies of changes (i.e. including ?+ and ?). The greatest difference is between models 2 (M2) and 3 (M3) (55 cases, corresponding to 28% of the total number of comparisons). The average difference computed considering all comparisons is 20%.

	M1	M2	M3	M4	M5
M1	0	39	42	50	29
M2	0	0	55	25	46
M3	0	0	0	40	34
M4	0	0	0	0	43
M5	0	0	0	0	0

b. Numbers re-calculated (from Table S3a) when tendencies are transformed in signs (i.e. ?+ becomes + and ?- becomes -). The largest difference is between models 2 and 3 (35 cases): their predictions differ in 17% of the comparisons. The average difference is 12%.

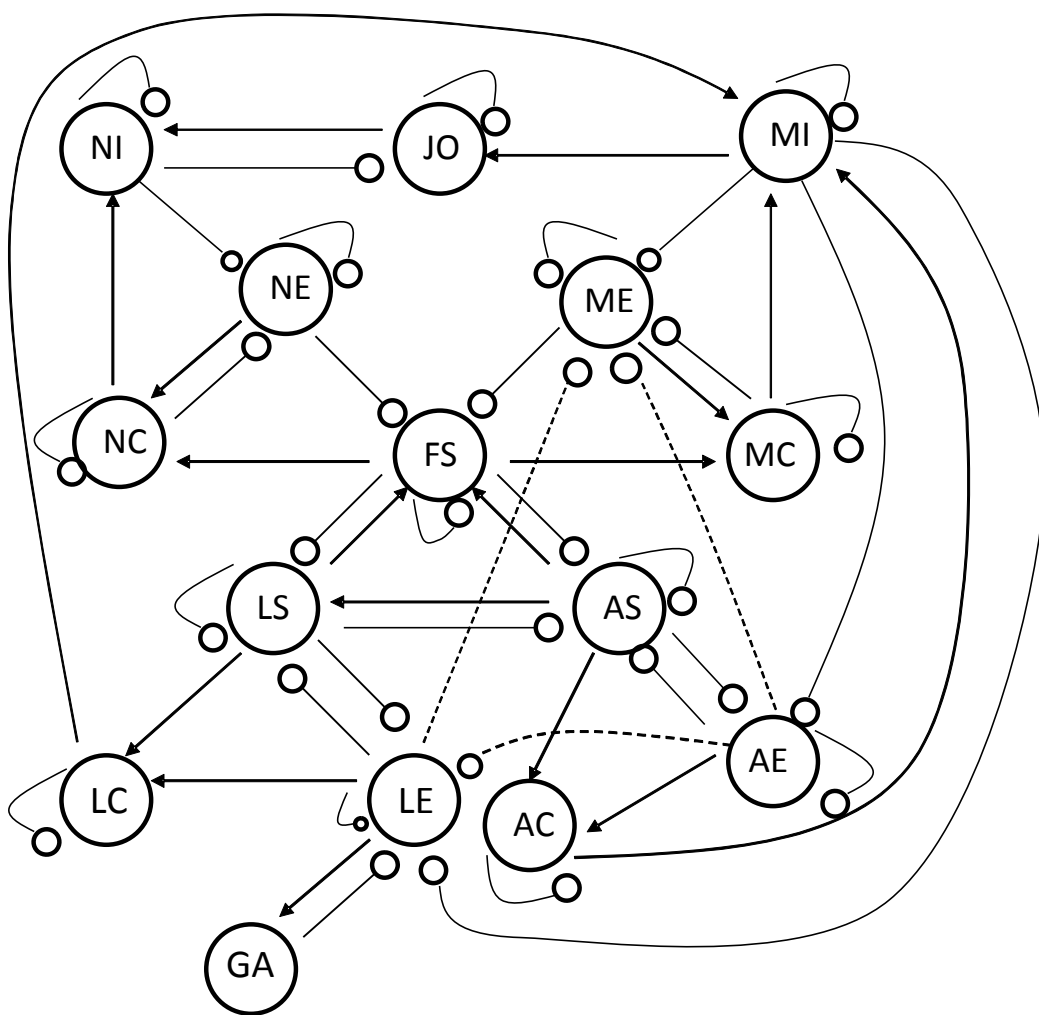
	M1	M2	M3	M4	M5
M1	0	25	28	31	15
M2	0	0	35	15	27
M3	0	0	0	24	24
M4	0	0	0	0	25
M5	0	0	0	0	0

**Table S4. Control over lobster effort through regulation.** In this model, control is exerted by a governmental agency (GA) that is represented in the graph as a “predator” on LE (lobster fishing effort). This represents the situation where a controlling factor (GA, in this case) reacts promptly to any variation in the level of effort, bringing it back to its original level. This control is possible because of the negative feedback between GA and LE and because GA is not self-damped. Without self-damping, GA responds only to LE. Its response is typical of a negative feedback that exerts a buffering effect. Moreover, LE remains unaffected by any input entering the system because GA, being non self-damped, makes the complementary feedback of all pathways to LE null. Therefore, GA protects LE against the effect of variations in the system. The table of predictions is reported below. The table shows that LE changes only for variations in the rate of change of the governmental agency which controls it.

	AS	AE	AC	LS	LE	LC	FS	ME	MC	NE	NC	MI	NI	JO	GA
AS	+	?-	?-	0*	0	0*	+	0*	+	-	?+	-	0*	?-	?+
AE	-	+	+	-	0	-	0*	-	-	0*	?-	+	+	+	-
AC	+	-	-	?+	0	?+	?+	+	+	?-	0*	-	0*	?-	+
LS	-	+	?+	0*	0	0*	0*	-	?-	0*	0*	+	?+	?+	-
LE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+
LC	+	-	-	?+	0	+	?+	+	+	?-	0*	-	0*	?-	+
FS	?-	?+	?+	-	0	-	?+	?-	0*	?-	0*	?+	?+	0*	0*
ME	?+	-	-	+	0	+	0*	+	+	0*	0*	?-	0*	?-	?+
MC	+	-	-	?+	0	?+	?+	+	+	?-	0*	-	0*	?-	+
NE	?+	?-	?-	+	0	+	?-	?+	0*	+	+	?-	+	-	0*
NC	?-	?+	?+	-	0	-	?+	?-	0*	-	+	?+	+	-	0*
MI	+	-	-	?+	0	?+	?+	+	+	?-	0*	-	0*	?-	+
NI	?-	?+	?+	-	0	-	?+	?-	0*	-	-	?+	+	-	0*
JO	?-	?+	?+	-	0	-	?+	?-	0*	-	-	?+	+	+	0*
GA	?-	?+	?+	?+	-	-	0*	?+	0*	0*	0*	?+	0*	?+	?+

**Figure S1. Control over lobster effort through regulation (see Table S4).**







## Appendix S-B

### R code for simulations

The procedure for simulations and the code are illustrated in what follows.

Input needed:

- 1- tab.txt (the community matrix with values -1, 0, +1 has to be created in .txt format and called tab.txt).
- 2- names2.txt (this is a row vector that contains labels for the variables. They have to be the same used in the community matrix, namely the column heads, and in the same order as they appear along the rows or columns of the community matrix)

Functions:

Once in R space launch:  
> source ("com\_mat2.R")

Script: com\_mat2.R

```
#marcus<-matrix(c(-1,1,-1,0),nrow=2,byrow=TRUE)
#marcus<-matrix(c(-1,0,-1,0,0,-1,-1,-1,1,1,0,-1,0,1,0,0),nrow=4,byrow=TRUE)
#marcus<-matrix(c(-1,1,0,0,0,0,-1,1,0,-1,0,0,-1,1,0,1,0,0,-1,0,0,0,0,1,-1), nrow=5, byrow=T)

names<-scan("names2.txt", what=character(), sep=", " )

marcus<-read.table("tab.txt", col.names=names, row.names=names, sep=", " )

#colnames(marcus)<-names
#rownames(marcus)<-names

print("community matrix")
print(marcus)

ll<-length(marcus)
print("ll")
print(ll)

#library("Rgraphviz")
#rEG<-new("graphNEL", nodes=c(names), edgemode="directed")
# plot(rEG)

#for (i in 1:ll)
# for (j in 1:ll)
# { if (i==j) (rEG<-addEdge(names(marcus)[i], names(marcus)[i], rEG, 1))
# else if ((i!=j) & (marcus[i,j]==1)) (rEG<-addEdge(names(marcus)[i], names(marcus)[j], rEG, 1))
# else if ((i!=j) & (marcus[i,j]==-1)) (rEG<-addEdge(names(marcus)[i], names(marcus)[j], rEG, 1))
# }
# plot(rEG, recipEdges = "distinct")

library("LoopAnalyst")
mat<-scan("tab.txt", what=character(), sep=",")
mat_v<-as.vector(mat)
mat_c<-matrix(c(mat_v), nrow=ll, byrow=T)
```

```
mat_tc<-t(mat_c)
colnames(mat_tc)<-names
rownames(mat_tc)<-names
graph.cm(mat_tc, file="mat_tc.dot")
```

```
#library("network")
#g<-network(marcus, direct=T, hyper=F, loops=T)
#plot(g, usearrow=T, arrowhead.cex=2, loop.cex=3, vertex.cex=1, edge.col=4,
#plot.network(g, usearrow=T, arrowhead.cex=2, loop.cex=3, vertex.cex=1, edge.col=4,
# vertex.col=1, label=network.vertex.names(g), displaylabels=T, boxed.labels=F, label.lwd=3, label.pos=0)
```

Output is the community matrix

Launch:

```
>source ("func_LOOP_sugg2.R")
```

Script: func\_LOOP\_sugg2.R

```
## Community matrix in Levins' notation###
```

```
library("MASS")
Loop <- function(marcus) {

  ### initializing count###
#  print ("WARNING!!! MASS PACKAGE NEEDED")

  print("community matrix")
  print(marcus)

  names<-scan("names2.txt", what=character(), sep=", " )

  k<-1
  m<-0
  h<-0
  #####
  #community matrix as sign matrix: lev #
  #####
  #####MATRIX IS: a11, a21, a31,...ect. where
  # aij=dfi/dxj change in the growth function of i due to j!#####
  #1°es. Predator-Prey

  lev<-t(marcus)
  Det_m<-det(lev)

  print("Determinant")
  print(Det_m)

  dl<-sqrt(length(lev))
  dl2<-dl^2
  print("dl")
  print(dl)
```

```

# print(dl^2)

nacc<-as.vector(k, mode="integer")
nacc[1]=0

n_p<-as.vector(m, mode="integer")
n_m<-as.vector(m, mode="integer")
n_oo<-as.vector(m, mode="integer")

for (m in 1:dl2) {(n_p[m]=0) & (n_m[m]=0) & (n_oo[m]=0)}

n_plus<-as.vector(n_p, mode="integer")
n_min<-as.vector(n_m, mode="integer")
n_o<-as.vector(n_oo, mode="integer")

##### NUMBER OF RUNS
# ntent<-(length(lev)*100)
# ntent<-(length(lev)*500)
ntent<-(length(lev)*1000)
# ntent<-(length(lev)*5000)
# ntent<-(length(lev)*10000)

print(ntent)
#####

for (k in 1:ntent){

#####
#random matrix: casuale #
#####

casuale<-matrix(rep(0,dl2),nrow=dl)

##### RANDOM MATRIX GENERATION (NAME IS: casuale) in [1e-6,1]
for (i in 1:dl)
  for(j in 1:dl) casuale[i,j]<-runif(n=1,min=1e-6,max=1)

# print(casuale)

#####
#weighted matrix (on degree tot for each variable) #
#####

num=0

ww<-matrix(rep(NA,dl2),nrow=dl)

for(i in 1:dl)
  for(j in 1:dl){ww[i,j]<-(lev[i,j]*casuale[i,j])
  }

det_ww<-round(det(ww), digits=6)

eig_vre<-round(Re(eigen(ww)$values), digits=6)
eig_vim<-round(Im(eigen(ww)$values), digits=6)

```



```

for (y in 1:dl) {if (eig_vre[y]<0) (num=num+1)}

#####A MINUS SIGN IS INSERTED DURING MATRIX INVERSION TO TAKE INTO
ACCOUNT THE SIGN OF COEFF b=-dfi/dc #####

if ((num-dl)==0) {(nacc[k]=nacc[k]+1) & (inv_ww<-(-round(ginv(ww), digits=6))) & (vector<-
as.vector(inv_ww))
  for (m in 1:dl2)
    {if (vector[m]>0) (n_plus[m]=n_plus[m]+1)
      else if (vector[m]<0) (n_min[m]=n_min[m]+1)
      else if (vector[m]==0) (n_o[m]=n_o[m]+1)}
    }

round(ginv(ww), digits=6)

per_p<-round(matrix(c((n_plus*100)/nacc[k]), nrow=dl, byrow=T), digits=5)
per_m<-round(matrix(c((n_min*100)/nacc[k]), nrow=dl, byrow=T), digits=5)
per_o<-round(matrix(c((n_o*100)/nacc[k]), nrow=dl, byrow=T), digits=5)

v_p<-as.vector(per_p)
v_m<-as.vector(per_m)
v_o<-as.vector(per_o)

nacc[k+1]=nacc[k]

#####

}

ntot=nacc[k]

OUT <- as.list(rep(NA,5))

OUT[[1]]<-ntot
OUT[[2]]<-k
OUT[[3]]<-per_p
OUT[[4]]<-per_m
OUT[[5]]<-per_o

print("n° ACCEPTED MOVES")
print(OUT[[1]])
print("n° loops")
print(OUT[[2]])
print(" (%) + ")
colnames(OUT[[3]])<-names
rownames(OUT[[3]])<-names
print(OUT[[3]])
print(" (%) - ")
colnames(OUT[[4]])<-names
rownames(OUT[[4]])<-names
print(OUT[[4]])
print(" (%) 0 ")

```

```

colnames(OUT[[5]])<-names
rownames(OUT[[5]])<-names
print(OUT[[5]])

tab<-as.vector(h, mode="any")

for (h in 1:dl2) {
  if (v_o[h]==100) (tab[h]<-0)
  else if (v_p[h]>=75) (tab[h]<-"+")
  else if (v_p[h]<=25 & v_p[h]>=0) (tab[h]<-"-")
  else if (abs(v_p[h]-v_m[h])<=20) (tab[h]<- "0*")
  else if (25<v_p[h] & v_p[h]<40) (tab[h]<-"?-")
  else if (60<v_p[h] & v_p[h]<75) (tab[h]<-"?+")
  }

tab_m<-matrix(c(tab), nrow=dl, byrow=T)
tabella_predizioni<-t(tab_m)

### insert as external#####
colnames(tabella_predizioni)<-names
rownames(tabella_predizioni)<-names

print("tabella_predizioni")
print.noquote(tabella_predizioni)

}

```

Launch: >Loop(marcus)

Output is: community matrix, determinant, accepted moves (i.e. stable matrices), matrices of +, - and 0 sign and percentages for each predictions, table of predictions.