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Resistance and re-organization of an ecosystem in response to biological invasion: Some hypotheses

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ABSTRACT

Using a dynamic model of Lake Chozas developed by Marchi et al. (2011), we tested three hypotheses about recovery of the indigenous community and water quality after radical changes caused by introduction of an invasive allochthonous crayfish, *Procambarus clarkii*:

1. Can the lake resist the pressure of an invasive species, like *P. clarkii*, by adaptation?
2. Can the ecosystem recover when all the crayfish are removed and low phosphorus concentrations persist in inflow water?
3. Does the simulated recovery of submerged vegetation occur at a total phosphorus concentration below 100 mg TP m^{-3}, as estimated by Scheffer et al. (1993), Scheffer (1997), Jeppesen et al. (1998) and Zhang et al. (2003)?

We obtained the following answers:

1. Lake Chozas can at least partly resist by adaptation. A combination of possible parameter changes could lead to a significant increase in eco-exergy.
2. Removal of the phosphorus represented by crayfish (by harvesting) implies complete recovery of the lake and its eco-exergy, albeit not necessarily with the same organisms having the same properties.
3. The expected hysteresis created by introduction and harvesting of crayfish is observed under the following conditions: phytoplankton dominance at total phosphorus $\geq$ about 200–250 mg TP m^{-3} and submerged vegetation returns at total phosphorus < 100 mg TP m^{-3}.

1. Introduction

Marchi et al. (2011) developed a dynamic model of Lake Chozas, a small shallow water body in León (NW Spain). Simulation of seasonal fluctuations in major lake elements by the model and direct measurements (Rodríguez et al., 2003, 2005) showed that the ecosystem lost internal information and complexity after the introduction of an invasive allochthonous crayfish, *Procambarus clarkii*. Benthic activity of the alien crustacean caused a decrease in submerged vegetation, favouring a transition from oligotrophic to eutrophic water quality. Lake Chozas underwent a rapid, drastic change in ecological conditions, going from dominance of aquatic plants to a phytoplankton explosion. The shift from clear to turbid water after the biological invasion was reflected by a decrease in eco-exergy and a corresponding increase in entropy of the indigenous community of the lake. Here we used the model to examine the possibilities of recovery of the lake after these major changes.

The planet Earth is like a super-organism and its ecosystems are like organs that self-organize and exchange energy and matter with each other. If an organ breaks down, planetary metabolism may be impaired but not necessarily collapse. Indeed, the Earth has survived enormous changes through mechanisms of self-adaptation to changes in chemicophysical conditions (Lovelock, 1972, 1974, 1990). Though ecosystems are smaller units, they

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too have mechanisms enabling them to survive adversities. For example, they may adapt to changes by resisting and re-organizing so as to survive (Tiezzi, 2003a). Biological invasions are one of many types of pressure that can upset the internal equilibria regulating biological cycles and food webs of ecosystems. Today, loss of biodiversity is a major problem, as invasions are increasingly frequent due to worldwide transport of goods and persons and the rise in mean global temperature caused by carbon dioxide emissions (Occhipinti-Ambrogi and Savini, 2003).

Particular combinations of parameters favour adaptation of invasive species to foreign ecosystems without impairing ecosystem complexity. Though these parameters vary from case to case, Marchi et al. (2010) postulated that the invader may become integrated in a foreign ecosystem, establishing a pseudo-equilibrium that enables it to survive and the ecosystem to conserve many of its ontogenetic features. This hypothesis is also confirmed in other papers (e.g. Branch and Steffani, 2004; Zardi et al., 2008).

We used the previous dynamic model (Marchi et al., 2011) to examine three questions regarding lake recovery after invasion by the alien crayfish:

1. Can the lake resist the pressure of an invasive species, like *P. clarkii*, by adaptation?
2. Can the ecosystem recover when all the crayfish are removed and low phosphorus concentrations persist in inflow water?
3. Does the simulated recovery of submerged vegetation occur at a total phosphorus concentration below 100 mg TP m^{-3}, as estimated by Scheffer et al. (1993), Scheffer (1997), Jeppesen et al. (1998) and Zhang et al. (2003)?

The model was used to trace structural changes in time and to predict seasonal fluctuations in major elements. The dynamic model was also used to test two hypothetical scenarios that we considered fairly realistic and in line with the Gaia hypothesis.

The first question was answered by testing 480 realistic combinations of parameters: we changed the maximum growth rate of the major elements in the lake, proposing values in a reasonable range. The second question was tested by simulating the seasonal dynamics of the state variables for 10 years into the future after disappearance of *P. clarkii* from the lake, postulating complete restoration of sediment chemicophysical properties and water quality. For the third question, we regulated total phosphorus concentration in the water column to obtain a scenario representing the eutrophic characteristics of Lake Chozas after introduction of the exotic crayfish.

2. Recovery of the lake, eco-exergy as indicator

Living systems absorb low-entropy energy from the environment, self-organizing and evolving (Tiezzi, 2003b; Jørgensen et al., 2007). In this way, they keep themselves far from thermodynamic equilibrium, maintaining low internal entropy or high exergy with respect to the environment (Jørgensen, 2007a).

Exergy reflects the survival of organisms in ecosystems, as demonstrated by dynamic models. It is defined as the capacity of an ecosystem for work relative to the same system at thermodynamic equilibrium, i.e. without heterogeneity or gradients (Jørgensen, 2007b). Eco-exergy increases with increasing ecosystem complexity, biodiversity and organization.

In the present study we used eco-exergy to measure variations in biomass and information stored in Lake Chozas in two cases. In the first, we postulated that the ecosystem resisted the biological invasion of *P. clarkii*, so that the complexity of the indigenous community was not completely destroyed by the benthic activity of the crayfish. We expected to find eco-exergy dynamics that oscillated without immediately falling to very low values. In the second case, we postulated that the ecosystem recovered the internal information that characterized its complexity before introduction of crayfish. We expected an initial period of perturbation of the chemicophysical characteristics of the system followed by a slow increase in eco-exergy. We endeavoured to understand whether these hypotheses could be reasonable through dynamic graphs of seasonal fluctuations of major lake elements.

3. Materials and methods

3.1. Ecosystem resistance through adaptation

Changes in the parameters of a model are associated with different ecosystem performances. In the search for a set of variables allowing adaptation of the indigenous community of Lake Chozas under the grazing pressure and bioturbation of *P. clarkii*, we proposed various combinations. Table 1 shows the set of variables we used to simulate ecosystem resistance to biological invasion. The second line of the table shows values used to calibrate scenario 2 of Marchi et al. (2011), in which the alien crayfish had already been introduced into the lake.

The parameters combined were: maximum growth rate of crayfish (MaxG_Crayfish), submerged vegetation (MaxG_Psp), phytoplankton (MaxG_PA) and zooplankton (MaxG_PZ). In fact, different growths and survivals of major lake elements determined variations in phosphorus concentrations in the state variables, which could modify community structure. The values we chose for these combinations were in the normal range, as confirmed by different references (Jørgensen and Bendoricchio, 2001; Jørgensen et al., 1991, 2000; Charles Kerfoot, 1980).

We made 480 runs using the programme STELLA version 8.1.4, trying all possible combinations of the parameters proposed in Table 1. At each run we controlled peak and final eco-exergy. The best run was judged to be the one in which eco-exergy had the highest final value, with oscillations indicating ecosystem resistance to perturbation (benthic activity of crayfish). In a previous study, the trend of eco-exergy after introduction of the crustacean decreased slowly and constantly in time (see Marchi et al., 2011).

3.2. Re-organization of lake ecosystem after biological invasion

To test re-organization of Lake Chozas after hypothetical disappearance of the crayfish, we first decreased the presence of the invader in the scenario to limit its impact on the indigenous

Table 1
Combination of variables used to simulate ecosystem adaptation.

MaxG_Crayfish (mg P m^{-3} per day)	MaxG_Psp (mg P m^{-3} per day)	MaxG_PA (mg P m^{-3} per day)	MaxG_PZ (mg P m^{-3} per day)
0.25[a]	2.00[a]	0.50[a]	0.40[a]
0.30	1.50	0.30	0.30
0.40	1.00	0.80	0.25
0.20	2.50	1.00	0.50
0.50		1.20	
0.10			

[a] Parameters used for calibration of scenario 2 of the dynamic model of Lake Chozas (Marchi et al., 2011).