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Transitional regimes as early warning signals in resource dependent competition models

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ABSTRACT

In this paper a question of "how much overconsumption a renewable resource can tolerate" is addressed using a mathematical model, where individuals in a parametrically heterogeneous population not only compete for the common resource but can also contribute to its restoration. Through bifurcation analysis a threshold of system resistance to over-consumers (individuals that take more than they restore) was identified, as well as a series of transitional regimes that the population goes through before it exhausts the common resource and thus goes extinct itself, a phenomenon known as "the tragedy of the commons". It was also observed that (1) for some parameter domains a population can survive or go extinct depending on its initial conditions, (2) under the same set of initial conditions, a heterogeneous population survives longer than a homogeneous population and (3) when the natural decay rate of the common resource is high enough, the population can endure the presence of more aggressive over-consumers without going extinct.

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1. Introduction

The identification of mechanisms responsible for the observed patterns of coexistence in populations whose survival is intimately connected to their ability to share a common resource is central to the study of ecological sustainability. The notion of niche construction provides but one way to organize and understand how populations can sustainably coexist with their resources. It is the goal of this paper to study this question using a simple resource-consumer framework.

The term "niche" was first introduced by Grinnell in 1917 [9] in his efforts to describe how an organism or a population responds to and competes for a common resource. The interactions of organisms or populations with available resources within their niche are not limited to consumption. Odling-Smee et al. [24] referred to the notion of "niche construction" in situations where organisms not only adapt in response to environmental pressures (for example, consuming the resource in the most efficient manner) but in the process also modify the environment. These adaptive interactions of consumers with their environment re-shape the niche to the needs of the communities that share the resource.

The focus of the discussion throughout this paper are consumer–producer systems (C–Ps), where the individuals that compete for resources also contribute differentially to "increases in the size of the pie". The carrying capacity of C–P systems turns out to be a function of the adaptive interactions between resources and the C–Ps. For example, through efficient handling of nutrients some plant species create and support positive feedback loops in their ecosystems and consequently, we observe that while in nutrient-poor environments plants produce slowly-decomposing litter, they grow rapidly and produce easily decomposable substances in nutrient-rich surroundings [11].

Processes of co-adaptation are observed in social environments as well. Individuals learn to respond to or get their clues from the "state" of the environment. Understanding the ramifications of these co-evolving interactions is particularly relevant to the study of how systems respond in times of crisis. Adaptive governance systems, for instance, self organize, drawing on individual characteristics and experiences of the people for the development of shared policies and principles [7,19,22,30].

The impact of co-evolutionary interactions is often a defining force. For example, earthworm burrows carry organic material into the soil, mixing it with inorganic material, creating in the process a basis for microbial activity, causing changes in the inner chemistry of the soil [23,25,29]. The environment (soil) has thus been altered over many generations, changing the evolutionary landscape and

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Table 1
Summary of variables and parameters used throughout the paper.

	Meaning	Range
$\widehat{z}$	Amount of renewable resource	$\widehat{z} \geqslant 0$
x_c	Population of clones competing for the resource	$x_c \geqslant 0$
γ	Intrinsic rate of resource growth independent of x_c	$\gamma \geqslant 0$
d	Per capita rate of natural resource decay	$d \geqslant 0$
e	Proportion of total resource consumed/restored	$e \geqslant 0$
b	Rate of resource consumption	$b \geqslant 0$
r	Per resource growth rate	$r \geqslant 0$
c	Amount of resource consumed	$c \in [\alpha, \beta]$
k	Efficiency of resource conversion to population biomass	$k \geqslant 0$
$\widehat{N}$	Total population size	$\widehat{N} \geqslant 0$
N_0	Initial population size	$N_0 \geqslant 0$
μ	Parameter of exponential distribution	$\mu \neq 0$
α	Lower boundary value of parameter c	$\alpha \geqslant 0$
β	Upper boundary value of parameter c	$\beta \geqslant 0$

Table 2
Sample parameter values.

	γ	d	e	r	b	k	N_0	z_0	μ	α	β
Set 1	1	1	1	1	1	1	0.6	0.1	10	0	2.5
Set 2	7.72	22	1	1	1	1	0.6	0.1	10	0	9.12

modifying the selective pressures faced by current generations [23]. Niche is therefore not a static concept but is an adaptive system in itself.

Recently, the question, ‘‘How can the ‘sustainability’ of alternative trajectories of human-environment interactions be usefully and rigorously evaluated?’’ was posed [5]. The need for the development of mathematical frameworks was explicitly addressed: ‘‘The central goal of such frameworks is to help us understand which uses of the natural environment (seen as natural capital) generate sufficiently large, wide-spread and long term benefits to human well-being that they can be valued as supporting sustainable development. (Having an answer to this challenge is what keeps ‘sustainability’ from being a euphemism for ‘environmental protection’.)’’.

The ability to understand and predict possible directions in which the consumer–resource may evolve is crucial in order to successfully achieve sustainable coexistence with common resources. It has been suggested that bifurcations in dynamical systems can correspond to ‘‘tipping points’’ in complex adaptive systems, which in turn may signal upcoming crises. The work presented in this paper will elaborate on this notion and present a framework within which one could in fact use transitional regimes in a dynamical system as early warning signs that may signal the need for increased efforts for resource preservation.

For these purposes a generalized model introduced by Krakauer et al. [16] is used, in which individuals within a population compete with each other for common renewable resources. First we investigate the question of the effects of the increases of resource (over) consumption on the entire population, identifying all possible dynamical regimes that the population can go through as it increasingly depletes its resources. Next, we evaluate what transitional regimes the population can go through when it is composed of both individuals that invest into the common resource, and those who over-consume. We conclude this paper with a discussion of the relationship between bifurcations and tipping points, and how one can use understanding of the system's dynamical regimes and bifurcation boundaries to forecast approaching collapse.

2. Model description

Consider the following generalization of the model introduced in [16], where a population of individual consumers x_c (from here on referred to as clones) compete for the common renewable resource $\widehat{z}$, which determines the carrying capacity of the population, in such a way as to not only consume the resource but to also be able to contribute to its restoration, i.e., contribute to increase of the common population carrying capacity:

$$\begin{cases} \frac{dx_c}{dt} = rx_c\left(c - \frac{b\sum_{\mathbb{A}} x_c}{k\widehat{z}}\right), \\ \frac{d\widehat{z}}{dt} = \gamma + \frac{e}{\widehat{z}+\sum_c x_c}\left(\sum_{\mathbb{A}} x_c(1-c)\right) - d\widehat{z}. \end{cases} \tag{1}$$

Each clone x_c is characterized by a value of the parameter c, with constant per capita birth rate r. The per capita death rate is proportional to $\frac{b\sum_{\mathbb{A}} x_c}{k\widehat{z}}$, where b is the rate of resource consumption, and k is the efficiency of resource consumption by each individual x_c and $\mathbb{A}$ is the range of possible values of c. In this formulation, $\frac{b}{k}$ denotes ‘‘competition efficiency’’ in obtaining the renewable resource $\widehat{z}$. Resources $\widehat{z}$ are restored naturally at constant rate γ, deteriorate at the rate $d\widehat{z}$ and can be replenished by the activity of x_c.

The rate of consumption/restoration of the common resource in response to the activity of x_c is modeled by the function $\frac{e}{\widehat{z}+\sum_{\mathbb{A}} x_c}\sum_{\mathbb{A}} x_c(1-c)$, where $\frac{\sum_{\mathbb{A}} x_c(1-c)}{\widehat{z}+\sum_{\mathbb{A}} x_c}$ denotes the total resource consumption/restoration rate by all the clones x_c, given both the competition with other clones $\sum_{\mathbb{A}} x_c$ and limitations on total resource accessibility; parameter e denotes the proportion of total resource that is consumed or restored, which can also be seen as per resource rate of restoration. As the number of consumers x_c increases, the amount of resource $\widehat{z}$ will increase or decrease depending on the value of the parameter $c \geqslant 0$.

The resource consumption/restoration parameter c is restricted to the interval $c \in [0, \beta]$, since within the frameworks of this model, the rate of niche-construction can neither be negative nor infinite. Letting $\beta = 1$ implies that the individuals in the population never consume more than they restore, making the population completely ‘‘altruistic’’. Letting $\beta > 1$ allows for the presence of overconsumers in the system, so $(1 - c)$ can take on negative values, which accounts for strictly consumerist behavior.

The solutions to the equation for population growth always remain positive. Solutions for the equation for $d\widehat{z}/dt$ can become negative when $c > 1 + \frac{\gamma}{e}$, since $\frac{d\widehat{z}}{dt}|_{z=0} = \gamma + e(1 - c)$, which is positive only when $c \in (0, 1 + \frac{\gamma}{e})$.

All the variables and parameters are summarized in Table 1; sample parameter values used for calculations are given in Table 2.

We first revisit the analysis of the case involving a population consisting of a single ‘‘average’’ clone type x_c interacting with a renewable resource in order to identify all the possible dynamical regimes for this system.

Letting $\widehat{N}(t) = \sum_{\mathbb{A}} x_c$ denote the total population size of the population leads to the following simplified version of System (1)

$$\begin{cases} \frac{d\widehat{N}}{dt} = r\widehat{N}\left(c - \frac{b\widehat{N}}{k\widehat{z}}\right), \\ \frac{d\widehat{z}}{dt} = \gamma + e\frac{(1-c)\widehat{N}}{\widehat{N}+\widehat{z}} - d\widehat{z}. \end{cases} \tag{2}$$

3. Analysis of the parametrically homogeneous system

3.1. System re-scaling

To simplify the analysis of System (2), we first re-scale it by setting $\widehat{N} = A \cdot N$, $\widehat{z} = B \cdot z$, $t = D \cdot \tau$. Taking $A = B = D = r^{-1}$, $\psi = \frac{k}{b}$, $\delta = \frac{d}{r}$, we end up with the following system of differential equations: