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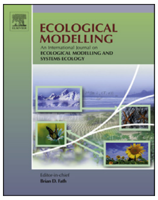

The effect of spatial heterogeneity and mobility on the performance of social–ecological systems

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A B S T R A C T

We use an agent-based model to analyze the effects of spatial heterogeneity and agents' mobility on social–ecological outcomes. Our model is a stylized representation of a dynamic population of agents moving and harvesting a renewable resource. Cooperators (agents who harvest an amount close to the maximum sustainable yield) and selfish agents (those who harvest an amount greater than the sustainable yield) are simulated in the model. Three indicators of the outcomes of the system are analyzed: the number of settlements, the resource level, and the proportion of cooperators in the population. Our paper adds a more realistic approach to previous studies on the evolution of cooperation by considering a social–ecological system in which agents move in a landscape to harvest a renewable resource. Our results conclude that resource dynamics play an important role when studying levels of cooperation and resource use. Our simulations show that the agents' mobility significantly affects the outcomes of the system. This response is nonlinear and very sensible to the type of spatial distribution of the resource richness. In our simulations, better outcomes of long-term sustainability of the resource are obtained with moderate agent mobility and cooperation is enhanced in harsh environments with low resource level in which cooperative groups have natural boundaries fostered by agents' low mobility.

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1. Introduction

This paper is concerned with the interlinked effect of mobility and spatial heterogeneity on the performance of social–ecological systems. Scholars have previously highlighted the effects of mobility and spatial structure on social dilemmas outcomes (e.g., prisoner dilemma game) and the evolution of cooperation (e.g., Nowak and May, 1992; Hauert and Doebeli, 2004). For more realistic approaches, however, it is important to take spatial dynamics into account in order to have a social–ecological perspective. Here, we develop an agent-based model to add a complex spatial setting to previous spatial social-dilemma models by including resource dynamics, in the form of a renewable resource, instead of the payoff matrix of social dilemma games. In doing so, we aim to analyze the levels of resource use, population growth, and cooperation in social–ecological systems.

The cellular automaton developed by Nowak and May (1992), in which agents interact with their neighbors in a two-dimensional spatial array, was the first attempt to include spatial structure in social dilemma games. In their model, Nowak and May found that spatial structure promotes cooperation by forming clusters and thereby reducing exploitation by defectors, in contrast with the spatially unstructured game, where defection is always favored. Subsequent studies also showed that limiting the interactions to local neighbors generally promotes the evolution and persistence of cooperation (Doebeli and Knowlton, 1998; Killingback et al., 1999). Under certain conditions, however, spatially structured games can be detrimental, like snowdrift-type interactions (Hauert and Doebeli, 2004; Hauert, 2006). The importance of the connectivity structure to understand the levels of cooperative behaviors has been demonstrated in a wide variety of agent-based models (for a review see Szabó and Fath, 2007). In addition to the spatial structure, the ability of individuals to move on the lattice enhanced cooperation compared to no mobile agents (e.g., Houston, 1993; Vainstein et al., 2007; Perc and Szolnoki, 2010; Smaldino and Schank, 2012). For example, sustained cooperation in a spatially structured Prisoner's Dilemma was obtained by Meloni et al. (2009) when agents were allowed to randomly move in a two-dimensional lattice while Helbing and Yu (2009) found that non-random mobility, in the form of success-driven migration, is essential for the stabilization and maintenance of cooperation.

Our goal here is to analyze how mobility and spatial heterogeneity affects the level of cooperation, as well as the

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resource and population growth, when we combined resource dynamics with spatial landscape structure and mobile agents. In ecological systems, spatial heterogeneity is essential to understand the functioning of the systems (Pickett and Cadenasso, 1995). For example, increased spatial heterogeneity, causing changes in landscape connectivity, affect, among other important ecological processes, animal population structures and community composition (Pickett and Cadenasso, 1995; Salau et al., 2012). Heterogeneity in social dilemmas is crucial to understand the evolution of cooperation. Cooperation can be facilitated when some agents have access to more resources than others (Kun and Dieckmann, 2013), when there is heterogeneities amongst players (Perc and Szolnoki, 2008), or when the payoffs amongst the players is not equally distributed (Perc, 2011). In social–ecological systems, the spatial distribution of resource richness might determine the pattern of processes such as resource use, habitat selection, population growth or cooperation of human communities.

We use an agent-based model to simulate a stylized representation of a dynamic population of cooperative and selfish agents moving and harvesting a renewable resource. By mobility we refer to the extent to which agents can move, which is related to the amount of information agents have about the system. Cooperative agents harvest an amount of resource close to the maximum sustainable yield while selfish agents may harvest an amount over the sustainable yield. Our main contribution to the study of the evolution of cooperation is to allow selfish and cooperative agents to harvest a renewable resource instead of the payoff matrix typically used in social dilemmas. The individual characteristics and behavior of agents determine the sustainable use or overexploitation of the resource. We analyzed the system's outcomes (resource, agents' occupational level, and cooperation) under several scenarios in which we vary the mobility of the agents and the landscape configuration (from homogeneous to very heterogeneous landscape).

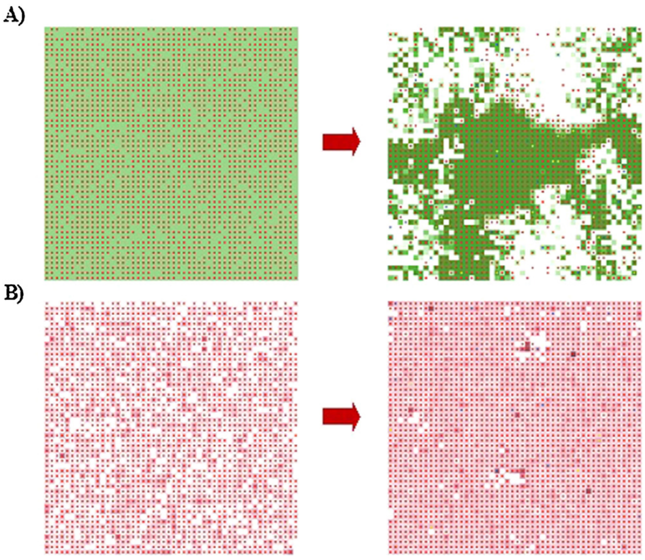

Fig. 1. Example of views of the default model at time step zero and 2500. (A) Resource: initially all the patches are settled to half of the carrying capacity. The image at the top left corner shows the homogeneous landscape at time step zero. Darker green means higher resource level; (B) population. Darker pink means higher density of agents. Initially 5000 agents are randomly allocated. Dots are agent. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2. Material and methods

2.1. Model description

The model is a stylized representation of a common-pool resource which is appropriated by a dynamic population of cooperative and selfish agents. The environment in which agents can move around and harvest is a renewable resource in a landscape of 50 cells × 50 cells (Fig. 1). Each time step, agents make decisions on movement, harvesting, storage of energy, and may reproduce or die. The agents can also imitate other agents' attributes if other agents are observed to be doing better (Fig. 2). Parameters and variables in the model represent units of energy.

Each cell contains a resource $R_{j,}$ which grows by the logistic growth function.

$$R_j - H_j + r \times R_j \times \left(1 - \frac{R_j}{K_j}\right)$$

where R_j is the resource level at patch j,H_j is the total resource harvested at patch j, r is the resource growth rate, and K_j is the carrying capacity of the resource at patch j.

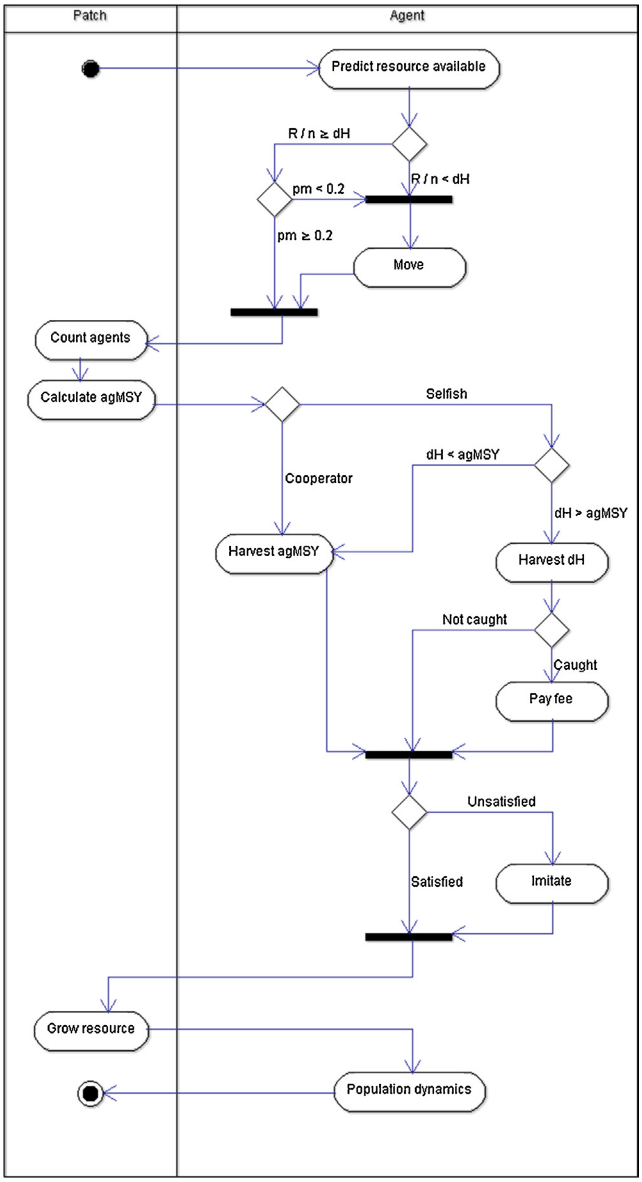

Fig. 2. Activity diagram (for a legend of parameters and variables see Table 1).