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

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ABSTRACT

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.

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).

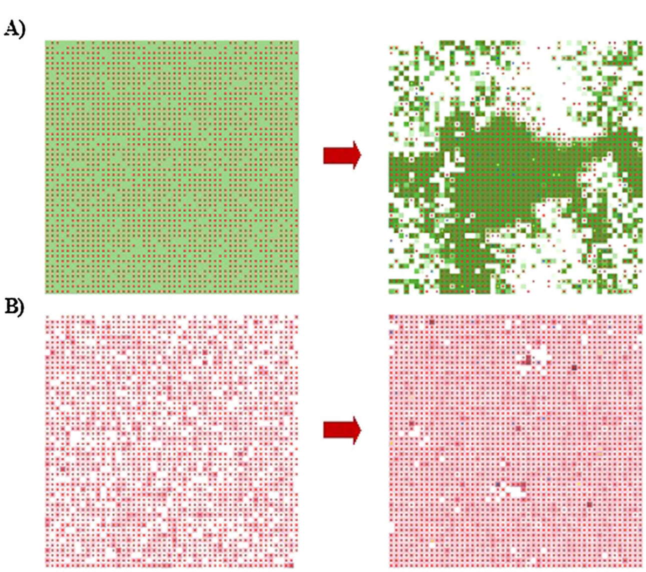

Fig. 1. Example of views of the default model at time step zero and 2500. (A) Resource: initially all the patches are settled to half of the carrying capacity. The image at the top left corner shows the homogeneous landscape at time step zero. Darker green means higher resource level; (B) population. 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.

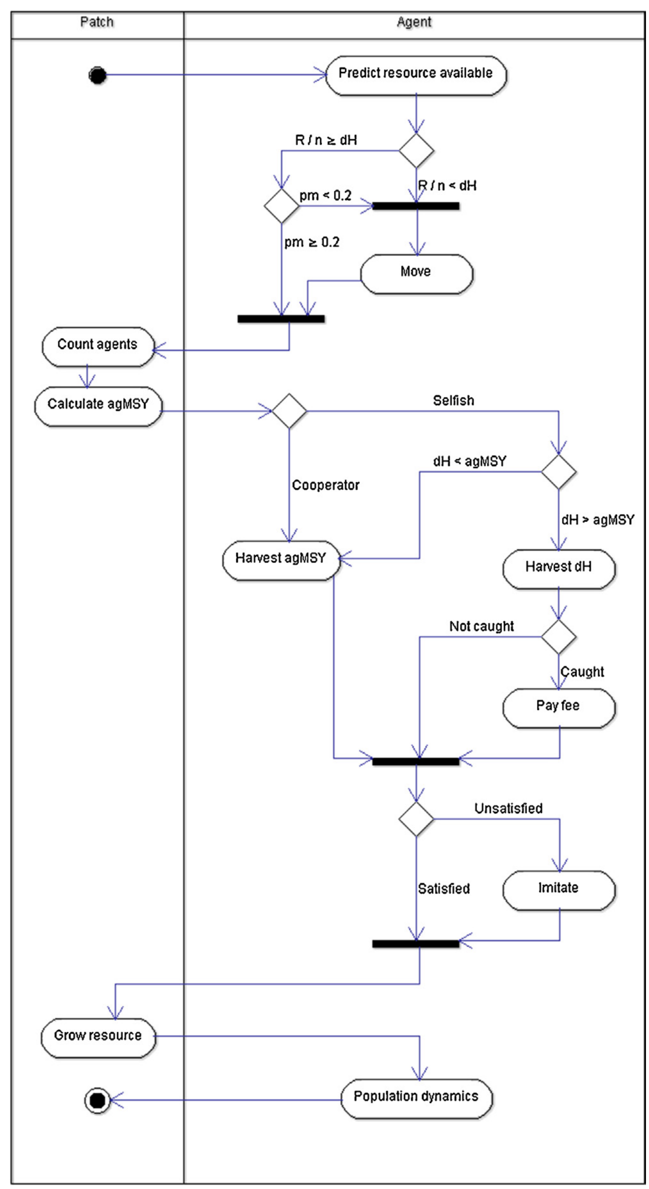

Fig. 2. Activity diagram (for a legend of parameters and variables see Table 1).

Each patch might have from 0 to n agents (Fig. 1). Institutional arrangements, like property rights, are not included.

We distinguish two behavioral types among the agents. The cooperative agents define the harvest level based on the maximum sustainable yield (MSY). The selfish agents define the harvest level based on the maximum economic yield (MEY) and harvest more from the resource. The harvest level of a cooperative agent is therefore defined as an amount near to the maximum sustainable yield (x_S):

$$x_{sj} = \frac{K_j \times r}{8} / n_j$$

where K_j is the carrying capacity at patch j, r the growth rate of the resource, and n_j the number of agents at the patch j.

Selfish agents harvest more than x_S if the desired amount of resource (H_D) is higher than the x_S. The desired harvest level H_D is:

$$H_{Di} = \text{met} \times (1 + S_i)$$

where met is the energy spent in the metabolism. Agents vary in the amount they desired to harvest above the metabolism rate. The parameter S_i is between 0 and 1 so that the agent will meet the strict metabolism value with $S_i = 0$, or a maximum of double the metabolism rate with $S_i = 1$. H_D, met, and S represent units of energy.

With a certain probability (p_c), defined as a model parameter, agents who harvest more than x_S are caught and pay a penalty fee (F_i).

$$F_i = (H_{Di} - x_{sj}) \times 2$$

The value of F_i is 0 if agent i is not caught or harvests an amount equal or less than x_S. Thus, p_c affects the amount of energy storage by the cheater. As we will describe later, this affects the reproduction capacity of these agents.

Every time step, agents consider whether to stay or not within their cell. If the harvested amount does not satisfy their desired harvest level (H_D), agents may move to the nearest cell with the highest resource level. Besides movement due to dissatisfaction, agents can move to another random patch with a fixed probability (p_m). Movement costs the agent energy. Every time step an agent changes its location, its accumulated energy (E_t) is reduced a certain amount (C_{mov}).

Agents store energy that is not used for basic metabolism, movement or reproduction:

$$E_{t_i} = E_{t-1_i} + x_{it} - F_{it} - \text{met} - C_{mov} - C_{rep}$$

where, x_i is the amount of resource harvested by agent i in time step t, F_i is the fee imposed to agent i, met is metabolism, C_{mov} is the cost of movement and C_{rep} the cost of reproduction.

If the energy stored by an agent becomes 0 or lower, the agent will die. With a birth rate (b_r), agents will reproduce. Agents give birth to one offspring. Birth rate depends on the stock of energy of agents and a reproduction rate (μ) of 0.03:

$$b_r = \mu \times \left(\frac{Et}{100}\right)$$

Offspring will reproduce the attributes of its parent. Parent and hatchling share the stock of energy from parent. Offspring will be allocated at the nearest patch (hr_{max}) with the highest resource level.

Every time step, agents can change their desired harvest level by imitating agents with the highest amount of accumulated energy located in their same cell. Whether an agent is cooperative or selfish can switch due to a small mutation with probability p_m.

Simulations are initialized with 5000 agents randomly allocated to cells on the landscape, with half of the population being selfish agents and half cooperative agents. An online appendix with the model code and model documentation using the ODD (overview, design concepts and details) protocol for describing individual- and agent-based models (Grimm et al., 2006; Grimm and Railsback, 2005; Grimm et al., 2010) can be found at www.openabm.org/model/3976/version/1/view The model is implemented in NetLogo 5.0 (Wilensky, 1999; ccl.northwestern.edu/netlogo/).

2.2. Model experiments

The dynamics of the model are explored by a series of experiments in which we vary the mobility of agents and the

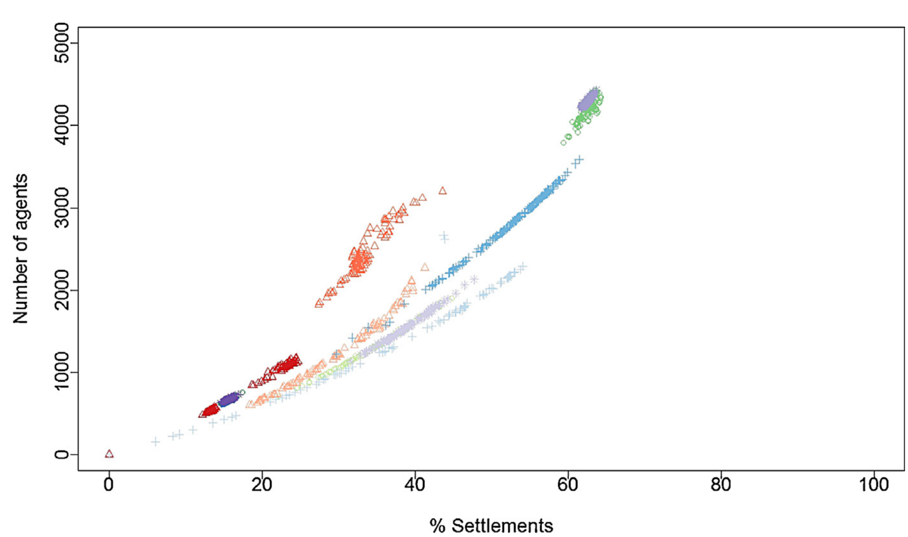

Fig. 4. Relationship between population level and settlements. Landscape heterogeneity: cross = homogeneous, star = uniform, circle = normal, triangle = exponential. Move capacity: light colors = 1, intermediate colors = 5, dark colors = 25. (For interpretation of the references to colorr= in this figure legend, the reader is referred to the web version of this article.)

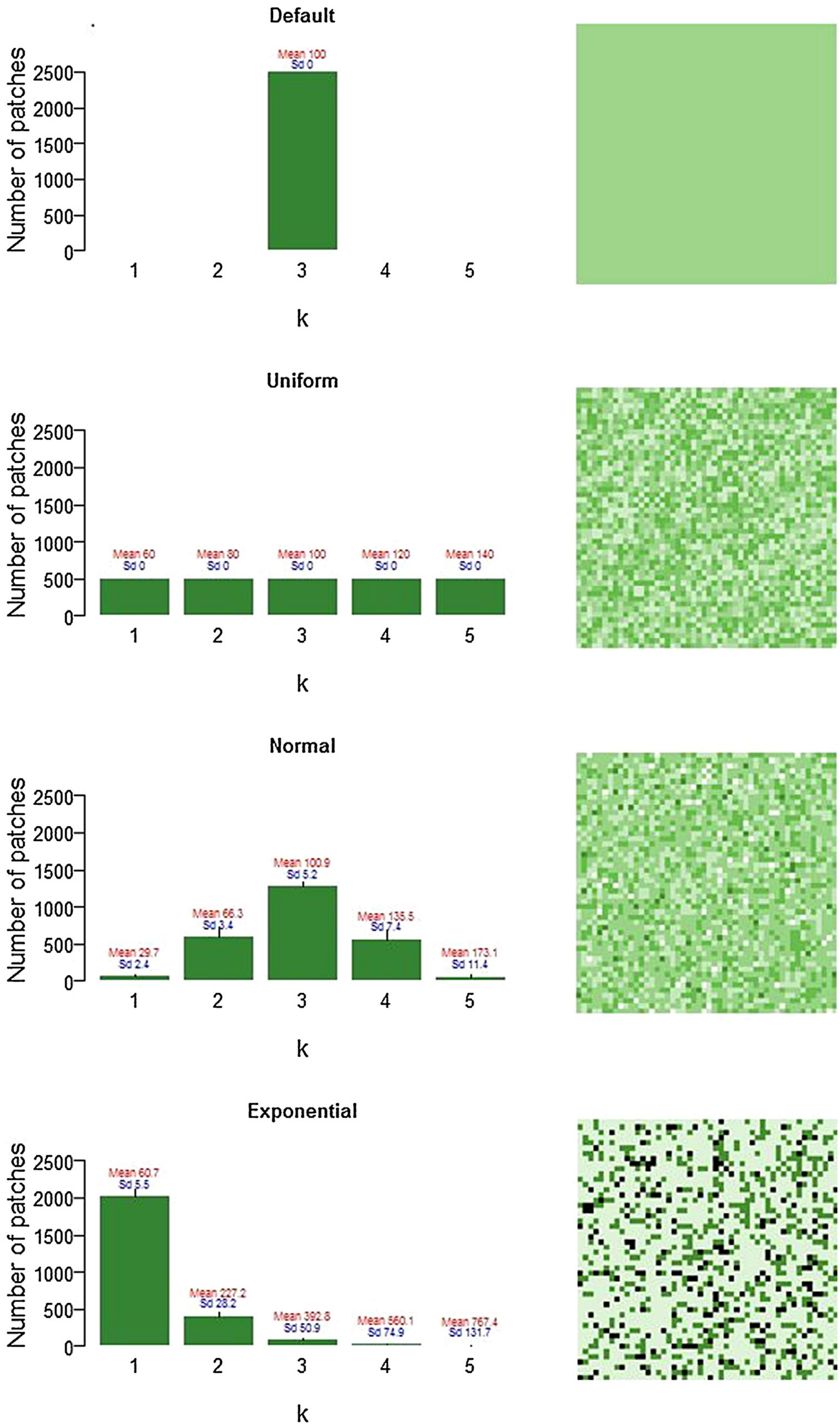

Fig. 3. Landscape structure. Graphs show the number of patches in the system for each carrying capacity of the resource (k). The mean is given in red and the standard deviation for 100 runs is given in blue. The right side of the figure shows the resource view of the model at time step zero for each landscape structure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Variables and parameter definitions of the model and parameter values of the default setting.

Parameter	Description	Value
X_S	Sustainable harvest level	0–k
$\mathrm{ar}_{\max}$	Maximum distance around the patch where agent is located in which agent can set its potential destination	1,5,25
μ	Reproduction rate of agents	0.03
C_{mov}	Cost of mobility	0.6
C_{rep}	Cost of reproduction	$E_t/2$
H_{D}	Desired harvest level of agents	0–1
E_{t0}	Initial energy level of an agent	10
E_t	Accumulated energy of agents	>0
H	Total resource harvested at each patch	0–n
$\mathrm{hr}_{\max}$	Radius around patches as potential destinations for offsprings' settles	5
I_{a}	Probability of agents copying the attributes of other agents in the same patch	0.2
k	Carrying capacity of resource	100 for the homogeneous landscape
met	Metabolism of agents	0.3
n	Number of agents in patch	0–n
F	Amount paid by cheaters	0–1
$P(0)$	Initial population size	5000
p_{c}	Probability of catching a cheater	0–1
p_{m}	Probability of random movement of agents	0.2
R	Resource level of each patch	0–k
r	Growth rate of resource	0.075
S	Storage level of agents	0–1
W	Size of the lattice	50×50, 100×100
	Initial probability of being selfish	0.5

landscape structure. We ran 100 iterations for each experiment and each simulation runs for a period of 5000 time steps. Early exploration of our model revealed that around 100 simulations are necessary to reduce the variability of our statistics to an acceptable level. We used as indicators the average of settlements (i.e., percentage of occupied patches by at least one agent), resource levels, and proportion of cooperative agents in the population, over the 100 iterations during the last 1000 time steps. Previous simulations showed a high correlation between settlements and population level (i.e., number of agents), thus we used the number of settlements as an indicator of the outcome of the simulation instead of population (i.e., number of agents) because its value is comparable among different resource richness distributions. Fig. 4 shows the high correlation between population and settlements.

2.2.1. Mobility

To analyze how the mobility of agents affects the indicators, we compared the results when we ran the model for different move capacities of the agents. Move capacity ($\mathrm{ar}_{\max}$) is the size of the radius that defined the possible set of patches an agent can move to. We ran the model for an $\mathrm{ar}_{\max}$ of 1, 5, and 25. One means that agents can move to the neighboring patches, while a move capacity of 25 means that agents can move to any patch of the system. Previous simulations with move capacities of 3 and 10 indicated linear relationship between 1,3, and 5 and between 5, 10, and 25.

2.2.2. Landscape structure

We run our model for different landscape configurations, i.e., differences in the carrying capacity (K) of the resource between patches. We considered four different statistical distributions of K: homogeneous, uniform, normal, and exponential. In the homogeneous landscape, all patches are settled to the same K. To settle the rest of the landscape configurations, we first assigned a value to each cell according to a uniform, normal or exponential distribution. Then, we grouped the resulting values in five equal intervals. Finally, we assigned to these categories of cells a specific value of very low,

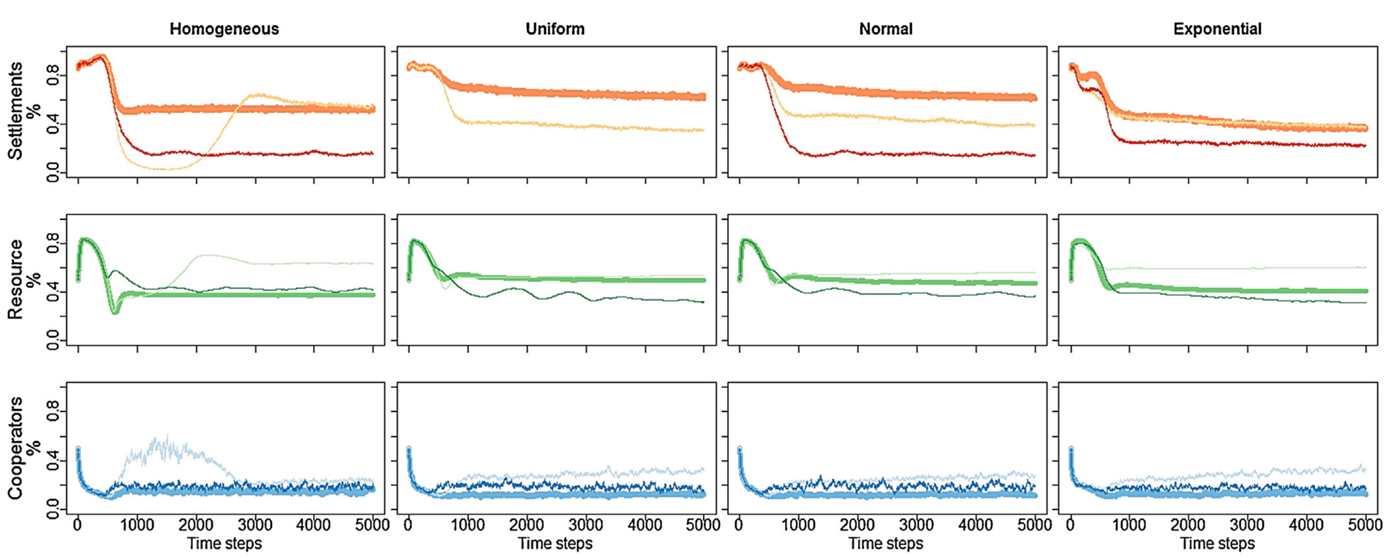

Fig. 5. Emergence value of settlements, resource level and percentage of cooperators in the population in one typical run of the model for the different landscape configurations. Lighter colors means a lower move capacity of the agents. Move capacities of 1, 5, and 25 are represented. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

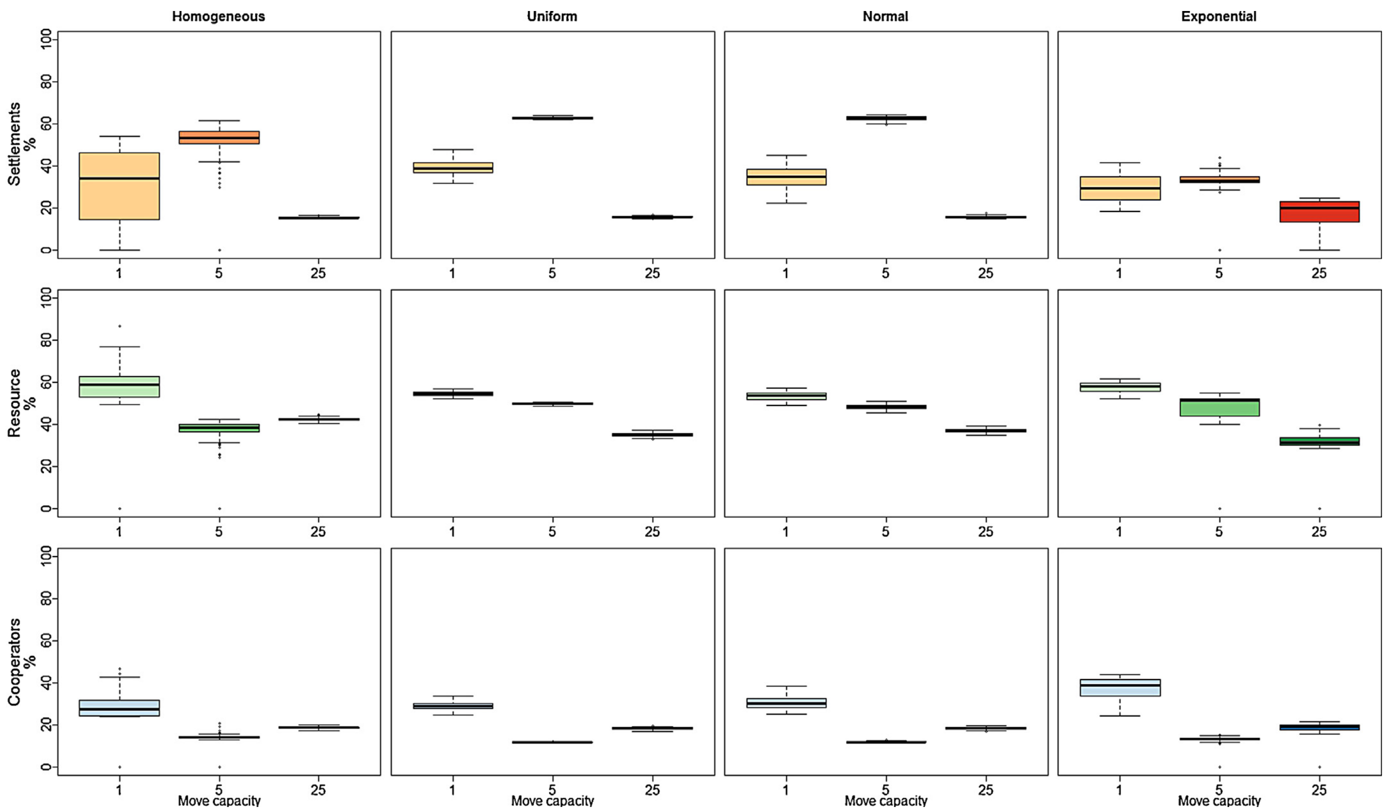

Fig. 6. Value of evolved attributes of the system over the last 1000 time steps of 100 runs for different move capacities of the agents and landscape configuration.

low, medium, high and very high *K*. To compare outcomes between landscapes configuration, we adjust these values so the total amount of resource on the entire landscape remains the same for the four landscape configurations (Fig. 3). We imported those results from the R statistical package (R Development Core Team, 2008) using the NetLogo extension r (Thiele and Grimm, 2010).

2.3. Sensitivity analysis

In the sensitivity analysis we varied the values of parameters from low to high values (Table 1) and ran the simulations for the different distribution of the resource richness considered. In particular, we varied the values of (i) the probability of agents copying (I_a), (ii) the probability of catching a cheater (p_c) and (iii) the size of the lattice (W) (Table 1). We use as indicator the average occupied patches, resource level, and number of cooperators over the last 1000 time steps of the 100 runs. We compared these results with results of the default models.

3. Results

Fig. 5 shows the value of settlements, resource, and cooperators in a typical round of the different landscape configuration. As Fig. 5 shows, systems with agents with a move capacity of one need more time to stabilize the system and after 3500 time steps all simulated systems are stabilized. We can observe some differences in the emergent parameter values based on both the move capacity of the agents and the landscape structure and that certain landscapes seem more sensitive than others to the mobility of the agents. Figs. 6–8 show how the mean value of the percentage of occupied patches (i.e., settlements), the resource level as well as the percentage of cooperators in the population varies between move capacities of the agents (Figs. 6 and 7) as well as landscape heterogeneity (Figs. 6 and 8).

3.1. The effect of mobility

In heterogeneous landscapes, lower occupation (i.e., number of settlements) and resource levels are obtained with high move capacity ($ar_{max} = 25$). With the same resource level, a low ($ar_{max} = 1$) and moderate ($ar_{max} = 5$) move capacity are able to support higher occupation levels in all the landscape configurations (Figs. 6 and 7). The highest percentage of occupied patches is obtained with a move capacity of five (Fig. 7). The resource level decreases as the move capacity of agents increases for all landscape configurations except for the homogeneous landscape, which ended with slightly higher levels of resource with a move capacity of 25 than with a move capacity of five (Fig. 7).

Low move capacity of agents ended with a low percentage of occupied patches and high resource level, meaning that agents are not able to reach potential expansion areas (Fig. 7). Under this condition, cooperative agents persist more than selfish agents. The highest proportion of cooperators in the population is obtained with a move capacity of one. The less cooperative population is obtained with a move capacity of five (Fig. 7). Low mobile agents need to adapt to the local conditions since they have less chances to get to high resources patches. As move capacity of the agents increases, cooperation decreases. However, higher levels of cooperators do lead to higher resource levels and lower number of settlements. Since cooperative agents do not overharvest they can only move around the landscape in a sustainable manner if the resource levels remain high giving them sufficient extra sustainable harvest to pay for the movement costs. A higher population pressure will reduce the ability of cooperators to pay for its mobility.

Figs. 9 and 10 show the value of the evolved parameters for different richness values of the patches (k) when the resource is uniformly distributed in the landscape. With a move capacity of one and five, agents select to settle in patches with high k value

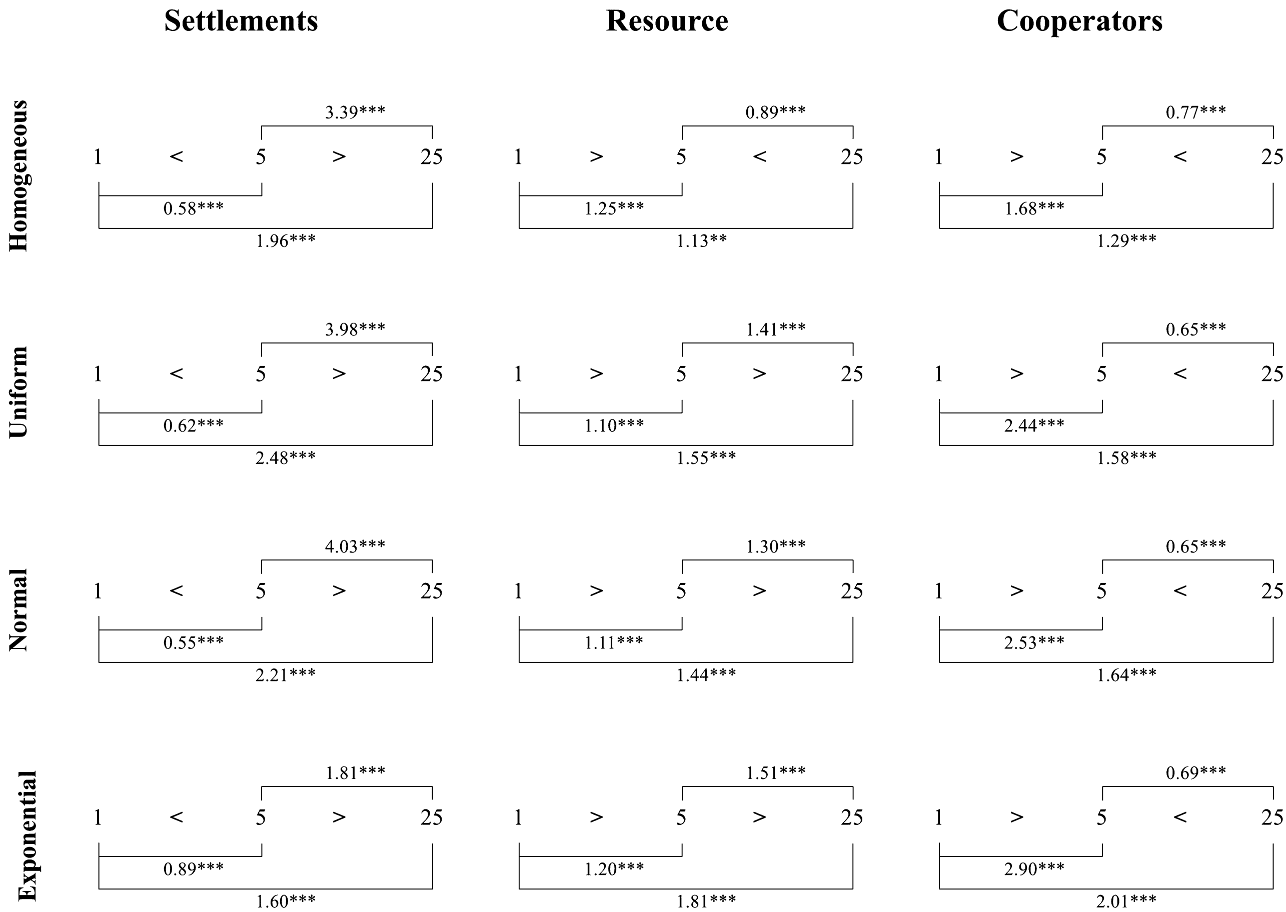

Fig. 7. Peer comparison (Student's *t*-test) of the average value of evolved parameters over the last 1000 time steps of 100 runs for different move capacities of the agents and landscape structure. Numbers represent the ratio between compared peers with the smaller move capacity over the greater. $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; $^{\text{n.s.}}p \geq 0.05$.

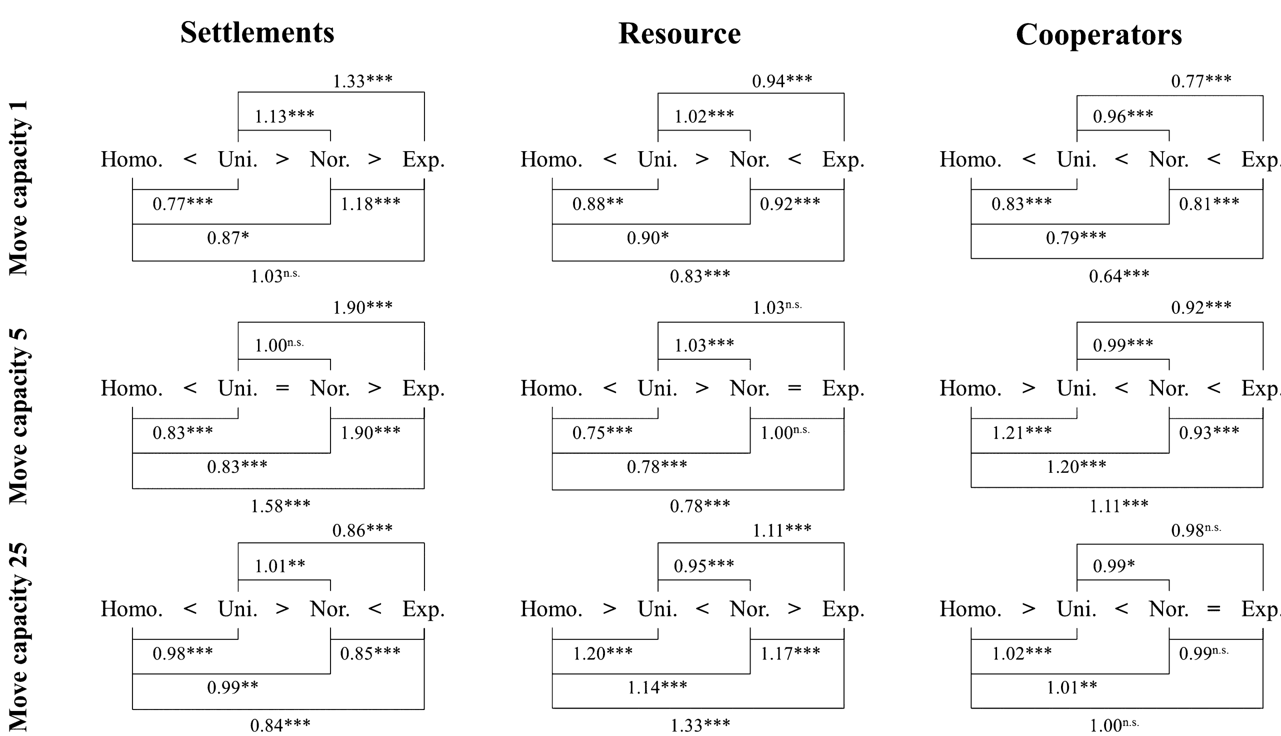

Fig. 8. Peer comparison of landscape structure with different move capacities of the agents. Results of the Student's *t*-test of the average value of evolved parameters over the last 1000 time steps of 100 runs are shown. Numbers represent the ratio between compared peers with the smaller landscape heterogeneity over the higher. $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; $^{\text{n.s.}}p \geq 0.05$.

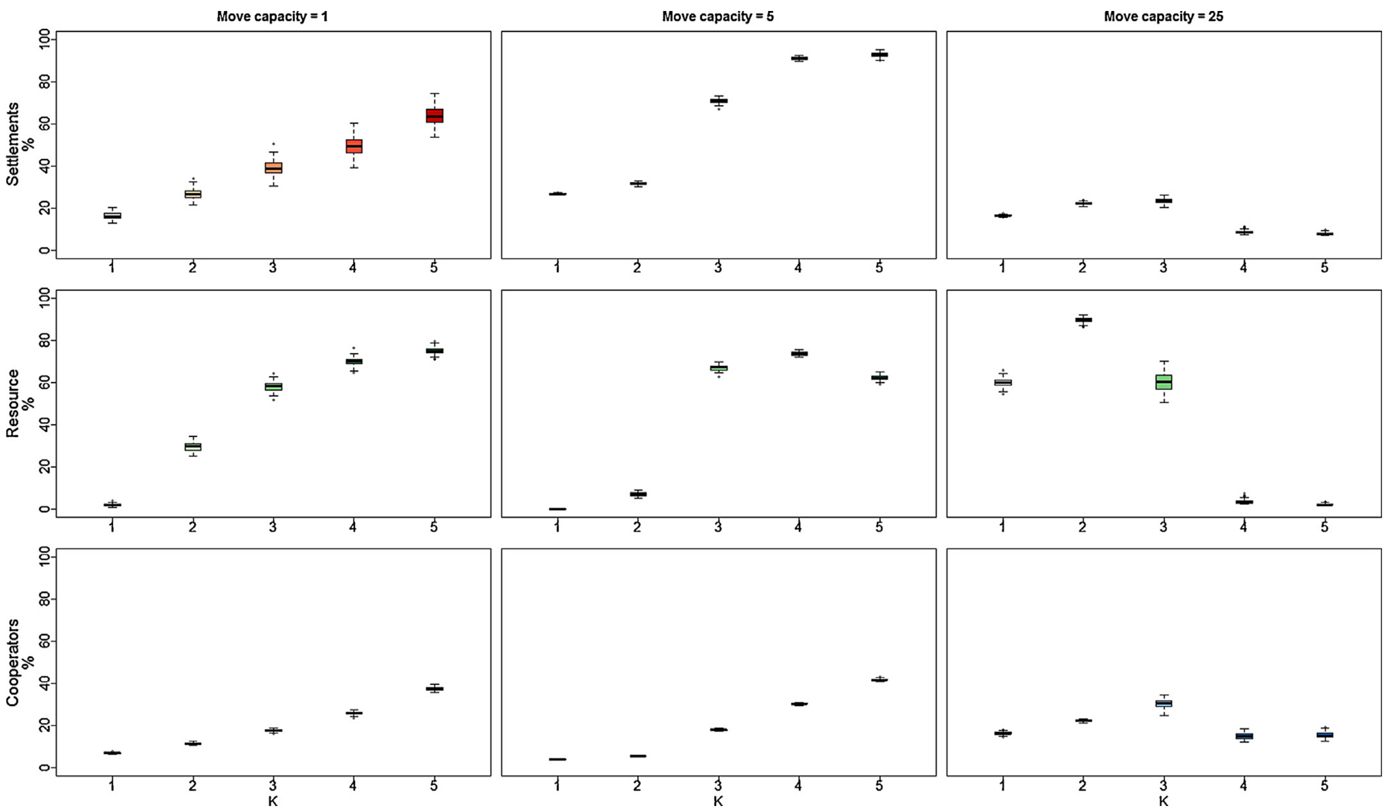

Fig. 9. Percentage of occupied patches, resource level, and proportion of cooperators in the population in patches with each value of K. Simulations are for a uniform distribution and move capacity of five. Lines represent the standard deviation. The first 4000 time steps are omitted.

($k > 3$). With a move capacity of five, the occupation level of those patches is close to 100%, while with a move capacity of one, the limited information of agents makes it more difficult for them to reach the best patches. However, with a move capacity of 25, patches with high k value ($k > 3$) had significantly lower levels of resource and occupation than patches with smaller k value. Agents with full information tend to move to patches with very high k value, hence those patches have lower stability because of overcrowding and overexploitation of local resources. On the contrary, patches with small values of k are more sustainable because they do not attract many agents. As Fig. 10 shows, in those patches where cooperation is lower, there is a worse performance.

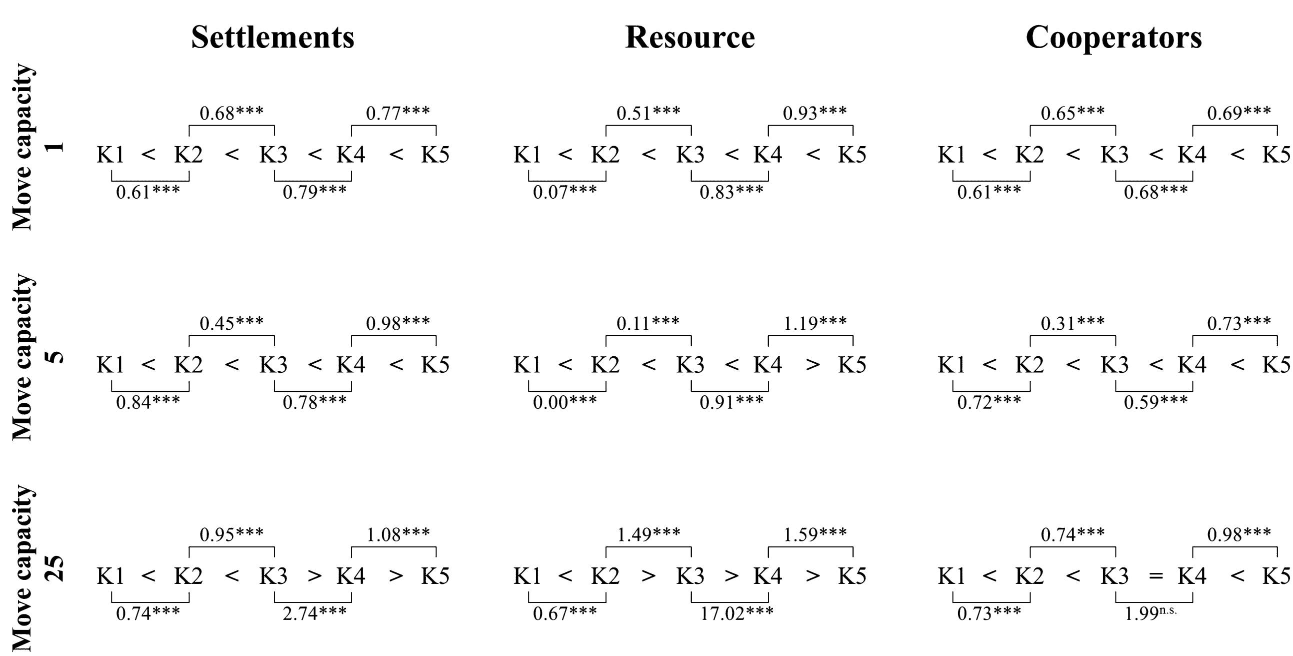

Fig. 10. Peer comparison of patches with different k values (resource carrying capacity) in a uniform distribution. Results of the Student's t-test of the average value of evolved parameters over the last 1000 time steps of 100 runs are shown. Numbers represent the ratio between compared peers with the smaller k over the higher. $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; $^{\text{n.s.}}p > 0.05$.

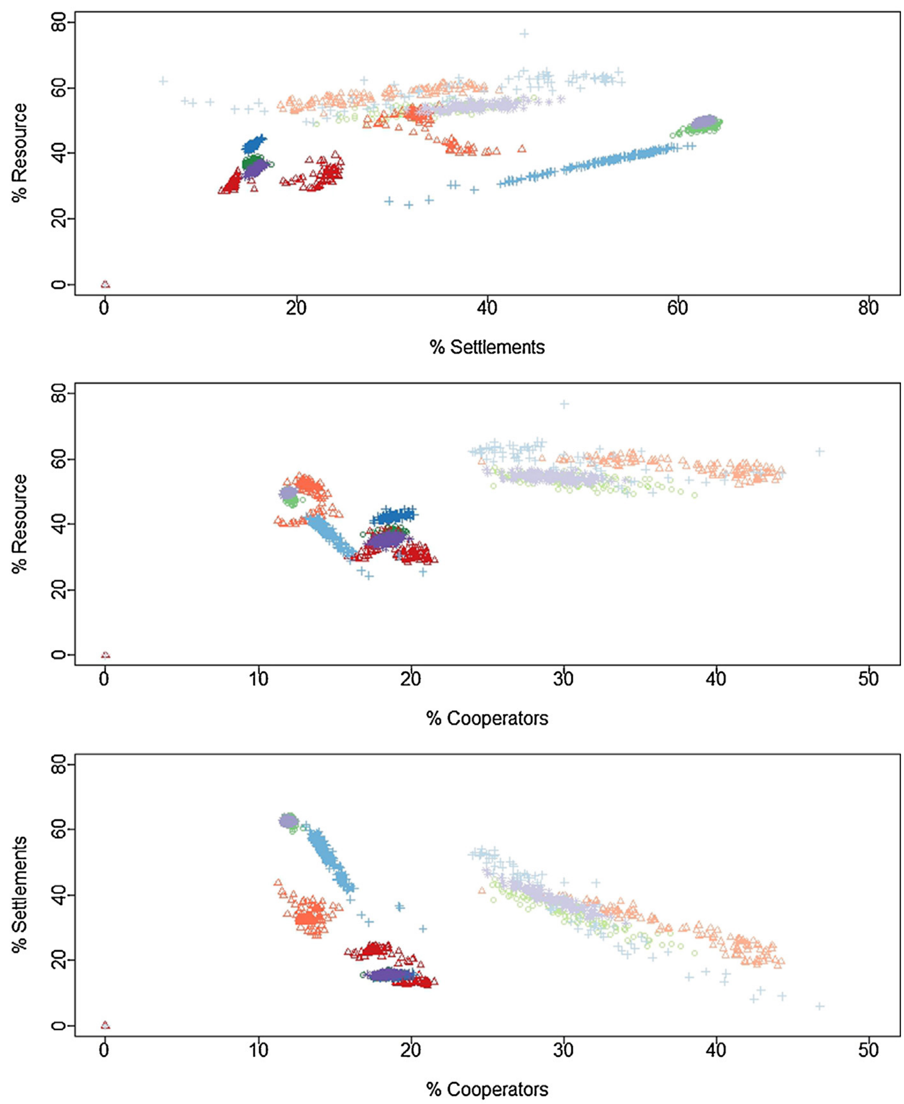

Fig. 11. Relationship of evolved variables. Landscape heterogeneity: cross = homogeneous, star = uniform, circle = normal, triangle = exponential. Move capacity: light colors = 1, intermediate colors = 5, dark colors = 25. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

On the contrary, with a move capacity of one, the cooperation level is higher in very rich patches. With a move capacity of five, cooperation increases as does the richness of patches.

3.2. The effect of landscape heterogeneity

As we will show below, the effect of landscape configuration on the evolved value of cooperation and resource levels highly depend on the combined effect of landscape and the move capacity of the agents (Fig. 8). In general, we observe that uniform and normal distributions of resource richness ended in the higher level of settlements but moderate levels of resource (Figs. 6 and 8). In addition, the effect of landscape configuration on cooperation levels is, although statistically significant, not as important as in the rest of indicators (Figs. 6 and 8). In general, higher cooperation levels are obtained in homogeneous or exponential landscapes when the move capacity of the agents is high or moderate. In contrast, cooperation decreases as landscape heterogeneity decreases when the move capacity of the agents is low (Figs. 5 and 8, see below).

3.3. The combined effect of mobility and landscape configuration

With low and high move capacity of the agents, landscapes with moderate resource heterogeneity had a moderate performance in terms of resource level (Figs. 6 and 8). The resource level is higher in exponential distributions of resource richness when the move capacity of the agents is low and higher in homogeneous landscape when the move capacity of the agents is very high.

Fig. 11 shows the relationship between the evolved variables for the different landscape configurations and move capacities of the agents and help in the understanding of the dynamics of the model. In general, Fig. 11 shows that the number of occupied patches increases as the resource does but higher resource levels do not lead to higher levels of cooperation. In addition, cooperation increases as the settlements decreases.

When the move capacity of the agents is high, the effect of landscape configuration decreases (Fig. 11). As shown in Fig. 11, the value of the evolved variables when agents have a high move capacity is more similar than when the move capacity decreases. Although statistically different (Fig. 8), when agents have a high move capacity, the effect of landscape heterogeneity on the

Table 2
Results of the sensitivity analysis. Average frequencies of settlements, resource level, and cooperators over the last 1000 time steps of 100 runs for different parameter (see Table 1) and initial conditions combinations and comparison with the simulations in different landscape configurations and with agents' move capacity settled to 5.

Parameter	Value	Resource distribution	Settlements		Resource		Cooperators	
			Mean	Sd	Mean	Sd	Mean	Sd
I_a	0.01	Homogeneous	0.85	0.00	0.65	0.00	0.38	0.00
		Uniform	0.74	0.00	0.65	0.00	0.39	0.00
		Normal	0.76	0.03	0.66	0.01	0.38	0.00
		Exponential	0.54	0.05	0.62	0.02	0.40	0.00
	0.2	Homogeneous	0.52	0.08	0.38	0.05	0.15	0.03
		Uniform	0.63	0.00	0.50	0.00	0.12	0.00
		Normal	0.63	0.01	0.48	0.01	0.12	0.00
		Exponential	0.34	0.04	0.48	0.05	0.13	0.02
	0.7	Homogeneous	0.00	0.00	0.00	0.00	0.00	0.00
		Uniform	0.60	0.01	0.48	0.01	0.07	0.00
		Normal	0.56	0.07	0.44	0.05	0.07	0.01
		Exponential	0.32	0.04	0.47	0.05	0.07	0.02
p_c	0.01	Homogeneous	0.00	0.00	0.00	0.00	0.00	0.00
		Uniform	0.00	0	0.00	0	0.00	0
		Normal	0.00	0.00	0.00	0.00	0.00	0.00
		Exponential	0.00	0.00	0.00	0.00	0.00	0.00
	0.3	Homogeneous	0.52	0.08	0.38	0.05	0.15	0.03
		Uniform	0.63	0	0.50	0	0.12	0
		Normal	0.63	0.01	0.48	0.01	0.12	0.00
		Exponential	0.34	0.04	0.48	0.05	0.13	0.02
	0.7	Homogeneous	0.77	0.00	0.91	0.00	0.33	0.00
		Uniform	0.74	0	0.87	0	0.27	0
		Normal	0.73	0.01	0.89	0.01	0.28	0.01
		Exponential	0.60	0.04	0.92	0.01	0.33	0.02
W	50×50	Homogeneous	0.52	0.08	0.38	0.05	0.15	0.03
		Uniform	0.63	0	0.50	0	0.12	0
		Normal	0.63	0.01	0.48	0.01	0.12	0.00
		Exponential	0.34	0.04	0.48	0.05	0.13	0.02
	100×100	Homogeneous	0	0	0	0	0	0
		Uniform	0.19	0	0.89	0	0.16	0
		Normal	0.47	0.15	0.43	0.09	0.16	0.08
		Exponential	0.35	0.07	0.43	0.08	0.14	0.05

occupational level is not as important as it is with a low, and especially with a moderate move capacity. With low or moderate move capacity of agents, landscapes with moderate resource distribution heterogeneity (uniform and normal) leads to a higher occupational level (Figs. 6 and 8). Also, the percentage of cooperators in the population is the same for all the landscape configurations but slightly lower for the uniform distribution of the resource (Fig. 8).

In general, uniform and normal distributions ended in similar results (Fig. 11). With these landscape configurations, the best relationship between settlement and resource is obtained. Move capacity of one leads to a high variability of results, even with situations of very high resources and very low settlements (Fig. 11) because there are less chances to occupy high resources patches.

3.4. Sensitivity analysis

We found that an increase in the frequency of imitation of agents (I_a) has a negative effect on the outcomes of the model (Table 2). For all landscape configurations, when I_a increases the number of occupied patches, the resource level and the proportion of cooperators in the population decreases (Student's t-test; $p < 0.001$). On the contrary, a change in the probability of catching a cheater (p_c) has positive consequences on the outcomes of the system (Table 2). In all landscape configurations, if the value of p_c is increased, then the number of settlements, the resource level and the proportion of cooperators in the population increases (Student's t-test; $p < 0.001$). Finally, an increase in the lattice size (W) has a significant effect on the outcomes of the system (Student's t-test; $p < 0.001$) (Table 2). If the value of W is increased, then the number of settlements increases in the exponential distribution, while the resource level increases in the uniform distribution. Also, when W increases, cooperation also increases for all the landscape configurations but for the homogeneous distribution of the resource. The relationship between resource level and landscape configuration is the same for both lattice size. However, when the value of W is increased, the number of settlements and cooperators are higher in the exponential and normal or uniform distribution of the resource and not in the homogeneous distribution as in the default model. Higher population increases allowed by a larger landscape, causes the depletion of the resource in the homogeneous distribution of the resource. Better outcomes in the heterogeneous distribution are obtained because population is able to stabilize since isolated settlements with cooperative solutions can persist.

4. Conclusions

We developed a stylized model of a social–ecological systems composed of agents moving in a variety of landscapes. Our purpose was to analyze the effects of mobility and landscape heterogeneity in a set of social–ecological indicators (i.e., agents' occupational level, resource level, and proportion of cooperators in the population). Our paper adds a more realistic approach to previous studies on the evolution of cooperation (e.g., Nowak and May, 1992) by considering a social–ecological system in which agents move in a heterogeneous landscape to harvest a renewable resource instead of the payoff matrix of social dilemma games.

We observe that the effect of both parameters (mobility and landscape heterogeneity) is highly intertwined. Therefore, the effect of landscape configuration on the evolved value of cooperation and population and resource levels is highly dependent on the combined effect of the landscape and the move capacity of the agents. Earlier studies with static social dilemma games showed that spatial structure increases cooperation in the prisoner dilemma game (Nowak and May, 1992) but inhibits cooperation in the snowdrift game (Hauert and Doebeli, 2004; Hauert, 2006). In accordance with previous studies of dynamic payoffs (Szabó and Fath, 2007), we found that natural resource dynamics have an important role in explaining levels of cooperation and resource use in social–ecological systems.

Our model shows that, in general, moderate agent mobility originated the best relation between settlements and resource, i.e., both high resource and high occupational levels are obtained. However, the resulting presence of cooperators in the population is low. Previous studies have shown a positive impact of resource adversity on cooperation due to resource unpredictability (Andras et al., 2007). In our simulations, cooperation is enhanced in harsh environments (i.e., low resource level) in which cooperative groups have natural boundaries fostered by agents' low mobility. Specifically, higher level of cooperation is obtained with low or high mobility and with homogeneous landscapes or in landscapes with an exponential distribution of resource richness. Low mobility makes population more cooperative but the low mobility leaves agents unable to expand to new rich areas, making the evolved resource level very high but the occupational level very low. Intermediate levels of cooperators are obtained with a high move capacity but the resource level is low compared with a moderate occupation level. This high move capacity is more threatening for the richest areas. Poorer areas were more sustainable because they did not attract many agents. As a consequence, the resulting agents' distribution was opposite of the expected ideal free distribution (Fretwell, 1972) and rich areas ended with lower resource levels due to the less sustainable behavior of agents. This selection process and differential agent behavior among resource conditions can lead to spatial pattern formation (Smaldino, 2013).

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