Mutual aid: When does resource scarcity favour group cooperation?

Etienne Delay, Cyril Piou

Mutual Aid: when does resource scarcity favour group cooperation?

Etienne Delay[a,b,c,*], Cyril Piou[d]

[a] *CIRAD UPR GREEN, F-34398 Montpellier, France*
[b] *GREEN, CIRAD, Univ. Montpellier, Montpellier France*
[c] *Laboratoire GEOLAB, UMR 6042 CNRS, Chaire "Capital Environnemental et gestion durable des cours d'eau", Université de Limoges, FLSH. 39E rue Camille Guérin, 87036 Limoges, France*
[d] *UMR CBGP, Univ. Montpellier, CIRAD, INRA, IRD SupAgro, 34398 Montpellier Cedex 5, France*

Abstract

Understanding the origins, conditions, advantages and limitations of cooperation in natural and social systems has motivated many investigations in the biological and social sciences. To investigate individual cooperative behaviour in the face of temporal and spatial heterogeneity of resources we considered a definition of cooperation at the same ontological level as competition. We define a cooperative behaviour when an agent acts upon one or more resource(s) with a beneficial result in at least one resource for a recipient of this action, and with a selection process for this behaviour on the side of the acting agent.

We implemented an agent-based model that represents the interactions of agents through their use of resources. With this model, we illustrated how scarcity of resources in space and time might create situations where cooperative behaviour is beneficial to individuals or to egalitarian groups.

Simulations highlighted that temporal scarcity as spatial scarcity of the resource procures advantages to egalitarian groups over competitive individuals. Additionally, the factors favouring equity among agents for the access to the resource promote the success of cooperation. Simulations also showed the limitations imposed by group size on cooperation in the context of a common-pool

*Corresponding author : etienne.delay@cirad.fr, phone : +33 467 593 881

management system.

The possibility of using indicators of (spatio-temporal) resource variability to characterize the potential for the emergence of cooperation is an interesting research objective for future work.

Keywords: Agent-based model, Spatial heterogeneity, Temporal heterogeneity, Resources, Cooperation, Competition.

---

1. Introduction

Competition has been a leitmotif process of selection in evolutionary theories of Darwinism since 1859 and in neo-Darwinism during the 20th century. Keddy (2001) synthesize competition as a negative interaction among organisms through the use of a same resource. For him,

> "All life forms consume resources such as water, oxygen, and nitrogen. This consumption reduces the supplies available for neighbors. In order to maintain access to resources, organisms must sometimes interfere with their neighbors. These three sentences summarize the state of affairs [...]. Without resources, organisms will die, and so the contest to find, harvest, transport, store and retain possession of resources is an essential part of the struggle for survival."(p.1)

These words, which open Keddy's book, are a synthesis of the resource-based definition of competition (Fig. 1(a)).

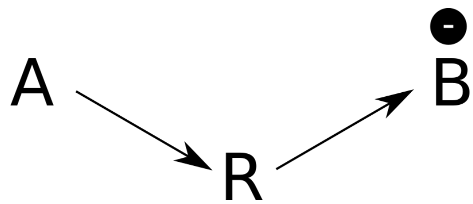
Scientific interest for cooperation and mutual aid begin more or less at the same time than Darwinism with the works of Kropotkin (1902). As a naturalist, he was among the first to argue about the potential effect of cooperation in the evolution of natural and human systems. Nowadays, cooperation is defined as :

> "a behavior which provides a benefit to another individual (recipient), and which is selected because of its beneficial effect on the recipient" (West et al., 2007) (e.g. fig. 1(b)).

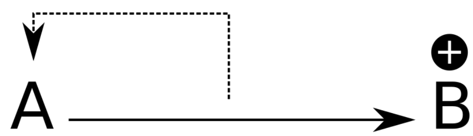
This definition is highly compatible with works on common-pools resources made by Ostrom (1990); Poteete et al. (2010), and research made in game theory (Axelrod and Keohane, 1985; Cohen et al., 2001). It does not base the interaction on a resource but on a behaviour. In all those works that investigate cooperation, the alternative to cooperation is generally considering behaviours such as "defection" or "betrayal". They set aside competition as it is not *per se* only a behaviour.

An ontological disjunction appears when we wish to use cooperation and competition together. For the ones working on competition what matters most is the interaction through or for the resources. For the others working on cooperation, the behaviour is put forth. Nevertheless, behind the usual benefits/costs matrix used in game theory, there is obviously one or several resources to consider. Some previous works in ecology proposed to consider resources as media of cooperation (Holland and DeAngelis, 2010). We follow the same line by considering a definition of cooperation at the same ontological level than competition. For that, we propose that cooperation occurs when an agent acts upon one or more resource(s) with a beneficial result in at least one resource for a recipient of this action, and with a selection process for this behaviour on the side of the acting agent (e.g. fig. 1(c)). We consider through this definition a large range of positive interactions. The selective aspect may be evolutionary in natural systems, but could also be through learning or coercive forces in animal or human societies (Hauert et al., 2007; Simon, 1990).

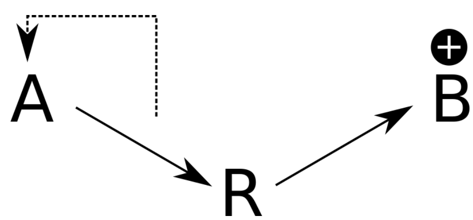
Setting the definition of cooperation in a resource-based context enables transdisciplinary comparisons and cross-fertilization among scientific fields. Indirect effects on common resources or on a shared "enemy" (Jeffries and Lawton (1984), enemy-free time or space act as a "resource") are included in this definition. The "multiple resources" aspect is important, particularly in complex systems where exchanges of resources are common (carbonic compounds vs. nutrients in plant interactions or host-symbiont interactions, survival favouring benefits vs. nutritional resources in animal interactions, economic capital vs. social or cognitive capitals in human societies, etc.).



(a)



(b)



(c)

Figure 1: Competition is a situation when agent A acts upon a resource (R) that generate a negative impact on a second agent B ((a) ; e.g.(Keddy, 2001)). Cooperation, as defined by West et al. (2007), is when a behaviour of A impacts B positively and a selection process exist on this behaviour (b). Our proposition (c) of definition of cooperation is to base the interaction upon a resource so that it is compatible with the formalism proposed in (a). The dashed arrows represent the selection process. The black arrows represent the interactions.

Understanding the origins, conditions, advantages and limitations of cooperation in natural and social systems has motivated many investigations in the biological and social sciences. In both animal and plant ecology the main research question is to understand the selective forces that create cooperative situations, focusing on individuals and genes. From these considerations, a corpus of complementary theories has been developed (from Hamilton (1964) to Allen et al. (2017)) to explain the conditions to observe cooperation situations in nature.

On the other hand, social scientists focus on cooperative organisations and institutions (Ostrom et al., 1994). Positive interactions are generally considered as an intrinsic characteristic of sociability. Hence, social scientists focus on understanding the social constructions and the mechanisms for the persistence of cooperation among interacting entities (Rogin-Anspach, 2002).

The two topics of "conditions" for and "mechanisms" promoting cooperation can be explored with many approaches: the social evolution theory, ecological approach, game theoretic approach, and social scientist approach (Bshary and Bergmüller, 2008). However, our definition of cooperation means that the conditions and mechanisms can be clearly defined in terms of resource variability and/or availability. It is then possible to explore the favourable environmental conditions for cooperation to outweigh competition. It is also interesting to look at how resource variability may promote selection at group level (West et al., 2007).

Agent-based models and simulations can be used to introduce constraints in a controlled world (Veldkamp and Verburg, 2004), and assess the impacts of different variables on the system under consideration (Delay, 2015). Some ABM studies have already explored the effect of resource heterogeneity on cooperation. For example, Bousquet et al. (1998), using a game theoretic approach explored the effect of resource spatial heterogeneity on the tragedy of the commons concept (Hardin, 1968). They showed that cooperative behaviours can be prosperous in a population when resources are not quickly renewed, creating heterogeneous local dynamics. The question of spatial heterogeneity and cooperation was further explored by Pepper and Smuts (2000). They illustrated that the spatial heterogeneity of a resource was a possible driver favouring the evolution of cooperative behaviours in natural populations through a balance among between-group and within-group selection.

In another multi-agent simulation, Smaldino et al. (2013) explored the effect of temporally variable environments on prisoner's dilemma types of interactions. They showed that cooperation could be beneficial in an extremely harsh environment, but after a long negative impact of that environment. Their temporal variation was homogeneous through space, and the cooperate-defect games were not directly resource-based. The same year Touza et al. (2013) used an ABM to explore cooperation emergence in red deer (*Cervus elaphus*) density management scenarios. They show that cooperation in spatial and temporal heterogeneous situations is highly context-dependent.

Complementing these studies, it appeared interesting for us to illustrate how resource scarcity in space and time could provide benefits for cooperative behaviour. Without simulating evolutionary process, we wished to explore in which resource conditions the cooperative groups may be selected. For this, we considered that equity among agents was a favourable condition for the groups through the appearance of potential feedback loop of selection at the individual level. This egalitarian access to resources suppose that all individuals within a cooperative group have homogeneous chances of being selected. Hence, we tested the hypothesis that resource variability provides benefits at both the individual and group level to cooperative use of resource. We explored this with an agent-based model setting cooperation among individuals depending on their spatial location and through their use of a theoretical resource. The resource-based approach of inter-individual interactions allows this model to go further than a game-theory approach on the impacts of agents on the resource and on the dynamics of this resource. However, this model was developed for illustration purpose (Edmonds et al., 2019) and do not claim to make any prediction on the real world.

2. Materials and methods

The model was motivated by reality but we chose to develop a purely abstract model inspired by the Epstein and Axtell (1996) "sugarscape" model. Hence, the resource here is "sugar", though the parallel with water management is possible. We used the Netlogo platform (Wilensky, 1999) to implement the model and R (Team, 2016) with RNetlogo (Thiele et al., 2012) to conduct our experiment plan. The formalization of the model description complies with the ODD (overview, design concept, details) description protocol (Grimm et al., 2006, 2010). [1].

2.1. Overview

2.1.1. Purpose

The objective was to illustrate how the spatial distribution of agents under spatial and temporal variability of resource accessibility affected their success in cooperating instead of competing. We were not interested in the emergence of cooperation and mutual aid *per se*. Rather, we explored in diverse socio-spatial and temporal configurations the benefits for individual agents of being part of a group sharing resources and the possibility for this group to create equity among agents.

2.1.2. Entities, state variables and scales

Entities : There were two types of entities in the model: individual agents and patches of resources. The individuals could not choose to be part of a group. The distance between agents defined their belonging to a group and cooperative behaviour. The agents were not mobile, and they could only harvest and use resources in their direct environment.
The patches were the spatial units of our model and represented small land portions.

[1] Our model development evolution and exploration scripts are available at [URL TO DOCUMENT AFTER ACCEPTANCE OF MANUSCRIPT]

State variables : As in the "sugarscape" model (Epstein and Axtell, 1996) each patch was characterised by the sugar resource present at each time step (ps_t). Additional characteristics were the maximum and minimum sugar potentially available in the patch and the initial sugar value.

Each agent had its own ID, its size (S, which reflected its fitness and need of resources), its cooperation expression (Ec), and a variable that stocked the available resource in the agent group accessible to all agents in that group (Sc).

Scale : The model was spatially explicit in a square space of 10000 resource patches (100×100). The space was with periodic boundary conditions (toroidal world). The interacting agents evolved over time with a theoretical time step corresponding to the time necessary to use their resource and change their size.

2.1.3. Process overview and scheduling

Our model was subdivided into four main processes (identified in detail in the submodel section for two of them, referred to with SM numeration). They were organized as follows for each time step:

- For patches :
  - *ReSugar* (SM1) regenerated the resource available in patches taking into account the seasonality and the actual resource value.
- For agents :
  - *Cooperate* prepared the agents that were able to cooperate to share their resource. Each cooperative agent shared its resource stock (Sc) with all its cooperative neighbours so that they all had the same amount across the group.
  - *Grow* (SM2) defined how agents could harvest, stock and use the resource.
- For patches:

– *Patch-diffusion* forced each cell to give an equal percentage share of its sugar to its eight neighbours with a diffusion rate (dr) fixed for each simulation between 0 and 0.5.

2.2. Design concepts

2.2.1. Basic Principles

To explore the effects of spatial and temporal variability in the resource as well as the effects of agent numbers and distributions, we compared simulations that were modified only for the criteria: *i)* without allowed cooperation *ii)* with allowed cooperation for some agents. With this benchmarking approach, we had the opportunity of exploring and understanding how the spatial and temporal availability of resources can influence the benefits of "*sharing capacity*" in theoretical groups.

2.2.2. Objective

Each agent tended to maximize its size by harvesting the resource, with harvest size proportional to agent size. Under cooperation, the agent's behaviour was modified to include sharing a fraction of the resource with its neighbouring agents.

2.2.3. Emergence

Depending on spatial resource heterogeneity, temporal resource heterogeneity and agent spatial configuration, a set of situations appeared in which cooperation and sharing was more efficient than being selfish in term of size incrementation.

2.2.4. Observation

Simulations of 2000 steps were analysed by summarizing agent size every 10 steps (see Fig. 2). For each observation, we summarized data in three groups: *i)* for all agents (gp1), *ii)* only grouped agents (gp2) and *iii)* only lone agents (gp3). For each of these groups we looked at the mean size of gp1, gp2 and gp3 to obtain information about the benefits these agents derived from use of the resource. As an indicator of inequity between agents, we computed the Gini index on the size distributions of gp1, gp2 and gp3. This index could take any value between 0, in the case of perfect equity, and 1 in the case of strong inequity.

2.3. Details

2.3.1. Initialisation

Our agents were all initialized with the same size ($S = 1$) and no shared resource stocks ($Sc = 0$). As our agents were not mobile, their initial positions were maintained within and between the simulations. These individual positions were read from one of 90 different spatial distributions generated to represent random, regular or clustered positions (see simulation plan sect. 2.4).

We used two types of space for the initialization of patches: *i)* a random distribution of the resource through space based on a uniform distribution and *ii)* the legacy sugarscape (Epstein and Axtell, 1996) resampled with the raster package (Hijmans, 2015). Once the patches received an initial sugar level (ops), we defined the minimum and maximum amount of the resource for each patch.

Once patches and individuals were initialized, a "scaling distance" (Sd) was computed to define the cooperative agents and create groups. The scaling distance was the average of the minimum distance from the nearest neighbours of each agent. Agents then received an Ec designation. Cooperative agents ($Ec = 1$) were the agents that had a minimum distance from their nearest neighbours that was smaller than the scaling distance. The others were not cooperative ($Ec = 0$). Hence, by construction, the nearest neighbour of a cooperative agent was also cooperative, and groups of mutually-cooperative agents were formed.

At the same time, a resugar factor (Rs), later implicated in the restoration of the resource, was computed as four times the number of agents divided by the number of patches. This recovering resource approach offered the opportunity of understanding group benefit without generating an additional carrying capacity effect other than the space map loaded during initialization.

2.3.2. Input data

There was no external input to the system once the simulation began.

2.3.3. Submodels

SM1 ReSugar : Resource regeneration was linked to the original space map through the value of sugar at initialization (ops) and an additional factor allowing for temporal heterogeneity in resource availability (Tv) creating seasonal cycles of 360 ticks (when $Tv = 1$). The computation of the new sugar content of a patch (ps_{t+1}) was given by:

$$ps_{t+1} = ps_t + Rs \times \frac{ops}{Mps} + Tv \times \frac{\sin(p) \times 40}{\sum_{x=0}^{x=180} \sin(x)} \tag{1}$$

where Rs was the scaling factor set at initialisation, ops was the initialized sugar level for this patch, Mps was the average of ops across all patches, p was a time counter reset to zero after 360 time steps and Tv (of value 0 or 1) was used to activate the temporal heterogeneity function. The iterative sum of $sin(p)$ and the scaling parameter of 40 were used to obtain seasonal variations of resource regeneration of +/- 20 points of sugar within half a season of 360 ticks. For mathematical stability, the range of ps was limited to 0 and 100.

SM2 Grow : In this procedure, every agent size ($S_{i,t}$ for agent i at time t) was increased or decreased following a growth rate ($rS_{i,t}$) in a Verhulst-type equation:

$$S_{i,t+1} = S_{i,t} + rS_{i,t} \times S_{i,t} \times \begin{cases} 1 - \frac{S_{i,t}}{maxSz} & \text{if} \quad rS_{i,t} > 0 \\ 1 - \frac{minSz}{S_{i,t}} & \text{if} \quad rS_{i,t} \leq 0 \end{cases} \tag{2}$$

where $maxSz$ and $minSz$ are the maximum and minimum possible sizes of the agents (arbitrarily fixed at 10 and 0.5), respectively. The growth rate $rS_{i,t}$ was computed for each agent as follows (see Appendix A for visualisation):

$$rS_{i,t} = maxR \times \begin{cases} \min\left(1, \frac{gS_{i,t}}{vR\times((1+maxR)^2-1)\times A_{i,t}}\right) & \text{if} \quad gS_{i,t} > 0 \\ \max\left(-1, \frac{gS_{i,t}}{vR\times(1-(1-maxR)^2)\times A_{i,t}}\right) & \text{if} \quad gS_{i,t} \leq 0 \end{cases} \tag{3}$$

where $maxR$ was the maximum growth rate (fixed arbitrarily to 0.1 in our simulations), vR was the necessary resource needed by an agent of $A = 1$ to keep itself at the same size (arbitrarily fixed at 2), $A_{i,t}$ was the area covered by the agent ($A_{i,t} = \pi \times (\frac{S_{i,t}}{2})^2$), $gS_{i,t}$ was the available sugar (from the Np patches under its influence (within area $A_{i,t}$) plus the shared stock $Sc_{j,t}$) allocated to growth by the individual i. This $gS_{i,t}$ was calculated for each agent taking into account the local resource and, if the agent was in a group (j), the value shared by the group ($Sc_{j,t}$):

$$gS_{i,t} = \begin{cases} \sum_k^{Np} ps_{k,t} - vR \times A_{i,t} + Sc_{j,t} \times C_2B & \text{if} \quad \sum_k^{Np} ps_{k,t} < vR \times A_{i,t} \\ \sum_k^{Np} ps_{k,t} - vR \times A_{i,t} + (1 - Sc_{j,t} \times C_2S) & \text{if} \quad \sum_k^{Np} ps_{k,t} \geq vR \times A_{i,t} \end{cases} \tag{4}$$

where $Sc_{j,t}$ is the resource shared by the group j, C_2S (*Coop. to Stock*) defines the proportion of the harvested resource pooling in the group's shared resource, C_2B (*Coop. to Burn*) is the proportion of the resource shared by the group available for each agent if its own harvested resource was not enough. The stock reserve of the group $Sc_{j,t}$ was depleted by each cooperative agent (i.e. each agent with property $Ec = 1$) if it was using the stock for growth ($Sc_{j,t} > 0$ and $\sum_k^{Np} ps_{k,t} < vR \times A_{i,t}$) (the $\rightarrow$ symbol means here that the variable was updated by each agent):

$$Sc_{j,t} \times (1 - C_2B) \rightarrow Sc_{j,t} \tag{5}$$

On the other hand, if the cooperative agent did not need the stock ($\sum_k^{Np} ps_{k,t} > vR \times A_{i,t}$), it added to it depending on the available sugar and the proportion fixed for all the cooperative agents for a simulation (C_2S) :

$$Sc_{j,t} + (\sum_k^{Np} ps_{k,t} - vR \times A_{i,t}) \times C_2S \rightarrow Sc_{j,t} \tag{6}$$

$Sc_{j,t}$ was bound to a maximum value arbitrarily fixed at 10 000 for mathematical stability. The non-cooperative agents ($Ec = 0$) did not use or update Sc. In this case $gS_{i,t}$ was then fixed at $\sum_k^{Np} ps_{k,t} - vR \times A_{i,t}$. All of this mathematical construction ensured that agents grew and decreased their size depending on the available resource, their size and the reserve of the group for cooperative agents. C_2S and C_2B parameters represent the ability of cooperators to stock part of their harvest and use a stocked part of their harvest in the event of spatial and temporal scarcity. These parameters were considered as social cooperation rules. The resource content of the Np patches affected by the growth of an agent were updated considering the agent's harvest. For a given patch u affected by an agent a and before being affected by an agent b:

$$ps_{u,t,a} - \frac{\sum_k^{Np} ps_{k,t}}{Np} \rightarrow ps_{u,t,b} \tag{7}$$

The random order of updating agents for each time step cancelled out the inequality in front of the use of shared patches.

The main global parameters of the model are listed in the Appendix B.

2.4. Simulation plan

As explained in the initialization section of the ODD, the spatial distribution of individuals and resource were factors that we explored to evaluate the benefits of cooperation in different resource availability and distribution scenarios. The other factors to explore were the resource diffusion rate (dr), the fact that resource replenishment varied over time (Tv) and cooperative behaviours (C_2S and C_2B).

Before looking at the cooperation situations, we ran each simulation without cooperation ($Ec = 0$ for all agents) in order to compare the situations with and without cooperation. For these simulations, 3 spatial distributions of agents (random, regular, clustered), 3 agent numbers (100, 506, 992) and 10 random replicates of each combination (distribution and number) were generated with R (Team, 2016) and the spatstat package (Baddeley et al., 2015) (see Appendix C). With these 90 fixed spatial configurations of agents, 2 resource distribution types (homogeneous or clustered), the 2 resource replenishment types ($Tv = 0$ or 1) and 6 diffusion rates values ($dr = 0, 0.1, 0.2...0.5$), the total number of runs was 2160 for situations without cooperation. For each run we recorded the

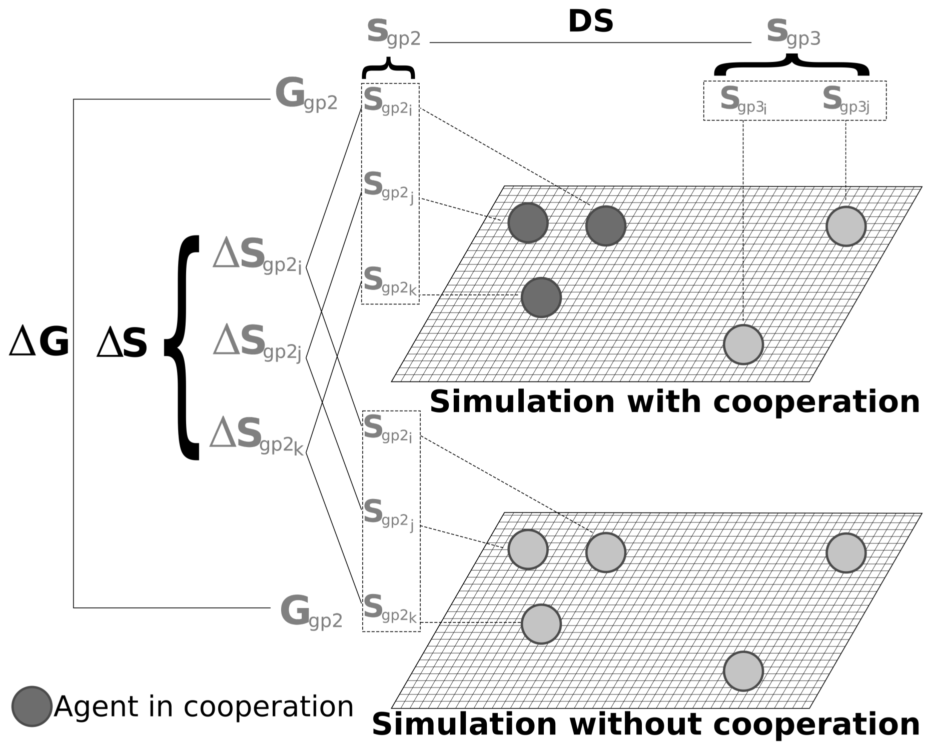


Figure 2: Explanation of the three indicators used to summarize the outcomes of simulations: ΔS, DS and ΔG. The dashed lines indicate the attributes of agents (S = size). The G measures the Gini index of sizes within a group of agents. The continuous lines indicate computations of difference. The curly braces indicate computations of average.

mean agent size and Gini index of size distribution in the three agent groups gp1, gp2 and gp3 (see section 2.2.4) during the second half of the simulation (from step 1001 to 2000).

The simulations with cooperation replicated the same situations but also allowed C_2S and C_2B to vary. Both parameters were fixed at 0.1, 0.5 or 0.9. For the resulting 19440 simulations with cooperation, the same indicators (mean agent size and Gini index for each of the three groups) were recorded. To summarize the effect of cooperation from all these simulations we focused on three indicators (Fig. 2).

The first one, ΔS, was an indicator of gain in size for the gp2 individuals with cooperative behaviour allowed. ΔS was computed as a difference among simulations without cooperation and with cooperation behaviour allowed for identical parametrisation. At each observation time (100 measurements in the second half of the simulations), for each individual of gp2 the difference in size with and without cooperation was computed. Then, the mean of these differences was computed per observation time. Finally, ΔS was the mean over time of these mean differences. This indicator was positive when cooperation made agents larger than when cooperation was not included and negative when agents lost size with the inclusion of cooperation.

The second indicator, DS, was a measure of the advantage in cooperating obtained by comparing the size of gp2 agents (cooperative individuals) and gp3 agents (non-cooperative individuals). It was computed as the mean over time of the difference between the mean sizes of cooperative individuals and the mean sizes of non-cooperative individuals. This indicator was positive when cooperative individuals were larger on average than non-cooperative agents.

The third indicator, ΔG, was a measure of the changes in the inequalities (size differences) between cooperative agents (gp2). ΔG was computed as the mean over time of the difference between the Gini index of a simulation with cooperation allowed and the Gini index of the corresponding simulation without cooperation. Negative values indicated that inequality increased with cooperation being allowed in the simulations. Positive values indicated a more equal distribution of sizes with cooperation than without.

To summarize all of these results and focus on which conditions made cooperation individually advantageous thus leading to better sharing of the resource, we extracted the simulations in which the three indicators ΔS, DS and ΔG were above 0 in at least 75% of the simulations in a given parametrisation. The choice to use ΔG as one of these indicators implies that cooperation needed to increase equity among cooperative agents to be considered beneficial. This egalitarian access to resources meant that all individuals within a cooperative group had an equal chance of being selected. This choice was made also to avoid the case where an average increase in the size of cooperative agents (shown by a positive

ΔS) is not due to benefits accruing only to one or a few individuals, which could then be seen more as a parasitic situation than as cooperation.

3. Results

In this section, we present some simulation results for the three different indicators regarding three different points of view. We finish this section with a summary of the conditions propitious to cooperative behaviour.

3.1. Cooperation vs. individualism depending on agent wealth

Focusing on the simulations with 506 randomly distributed agents and the ΔS indicator, we were able to look at the effect of the C_2S and C_2B parameters on the difference in success of gaining size for identical individuals between conditions where cooperation was allowed or not allowed. These differences in size were positive when cooperation was individually beneficial for the agents involved in cooperation. For each cooperation setting (combination of C_2S and C_2B) and spatio-temporal variation in the resource, we were able to identify a maximum gain in size of the cooperative agents with an optimal spatial diffusion of the resource (dr, Fig. 3).

Without temporal resource variation (Fig. 3 a-b), the gain in size for co-operators increased under intermediate values of tested resource diffusion (dr). With clustered spatial distribution of the resource (Fig. 3b) the gain in size increase for high C_2S and low C_2B. This latter result highlights the effect of spatial distribution of the resource on the agent's potential gain from cooperation. There was a combined effect of resource distribution and cooperation rules on optimum access to the resource. For example, with cooperation rules of C_2S of 0.5 and C_2B of 0.5, an optimum appeared at a spatial dr of 0.2 (Fig. 3a). This optimum shifted to a dr of 0.1 with a clustered spatial distribution of resources (Fig. 3b). But a C_2S of 0.9 and C_2B of 0.9 shifted the optimum dr back to 0.2 (Fig. 3b).

Temporal heterogeneity (Fig. 3c-d) clearly favoured the gain in size of co-operative agents and increased the variability of that gain depending on the resource access parametrisation (comparing Fig. 3c to 3a). The gain in size reached more than 0.1 for a dr of 0.2, a C_2S of 0.9 and a C_2B of 0.1 (Fig. 3c). The introduction of resource spatial clustering (Fig. 3d) led to even higher size gain for the same configuration of dr, C_2S and C_2B. High C_2S and low C_2B mean a fairly stable shared stock, allowing more temporal averaging of the cooperative use of the resource and hence high values of ΔS in the face of temporal scarcity. Different C_2S and C_2B parameters (e.g. $C_2S = 0.1$ and $C_2B = 0.5$) might however lead to very low gains in size.

The effects of spatial and temporal variability of resources in interaction with specific values of C_2S and C_2B illustrates how the "social" rules of cooperation can be used to compensate for the geographical determinism of resource availability and its spatial variability. The dr, C_2S and C_2B parameters correspond to different spatial and temporal averaging settings. The cooperation rules provide an averaging among cooperative agents but generate costs at the individual level. Increasing the resource diffusion (dr) increase the averaging of resource for all and at no explicit cost (see Appendix D for an illustration of the effect through time of dr). Hence, cooperation is most beneficial when averaging is necessary in the face of temporal or spatial scarcity and not provided already by a diffusion process. In other words, when the diffusion process is low and resources are clustered in space or time, the extra costs of cooperation is worth to let circulate faster this resource among cooperative agents, who then gain in size. In such cases, the high C_2S and low C_2B are the most successful.

3.2. Cooperative vs. non-cooperative behaviour in a cooperative world

The initial population size and spatial arrangement of agents had an effect on the difference in size between cooperative agents and non-cooperative agents in simulations with cooperation allowed. To illustrate this, we looked at constant social rules of cooperation C_2S and C_2B (both fixed at 0.5 in Fig. 4). In a random resource map without temporal resource variation (Fig. 4a), a regular agent distribution led to an almost identical size of cooperative and non-cooperative agents while clustered or random distribution of agents led to

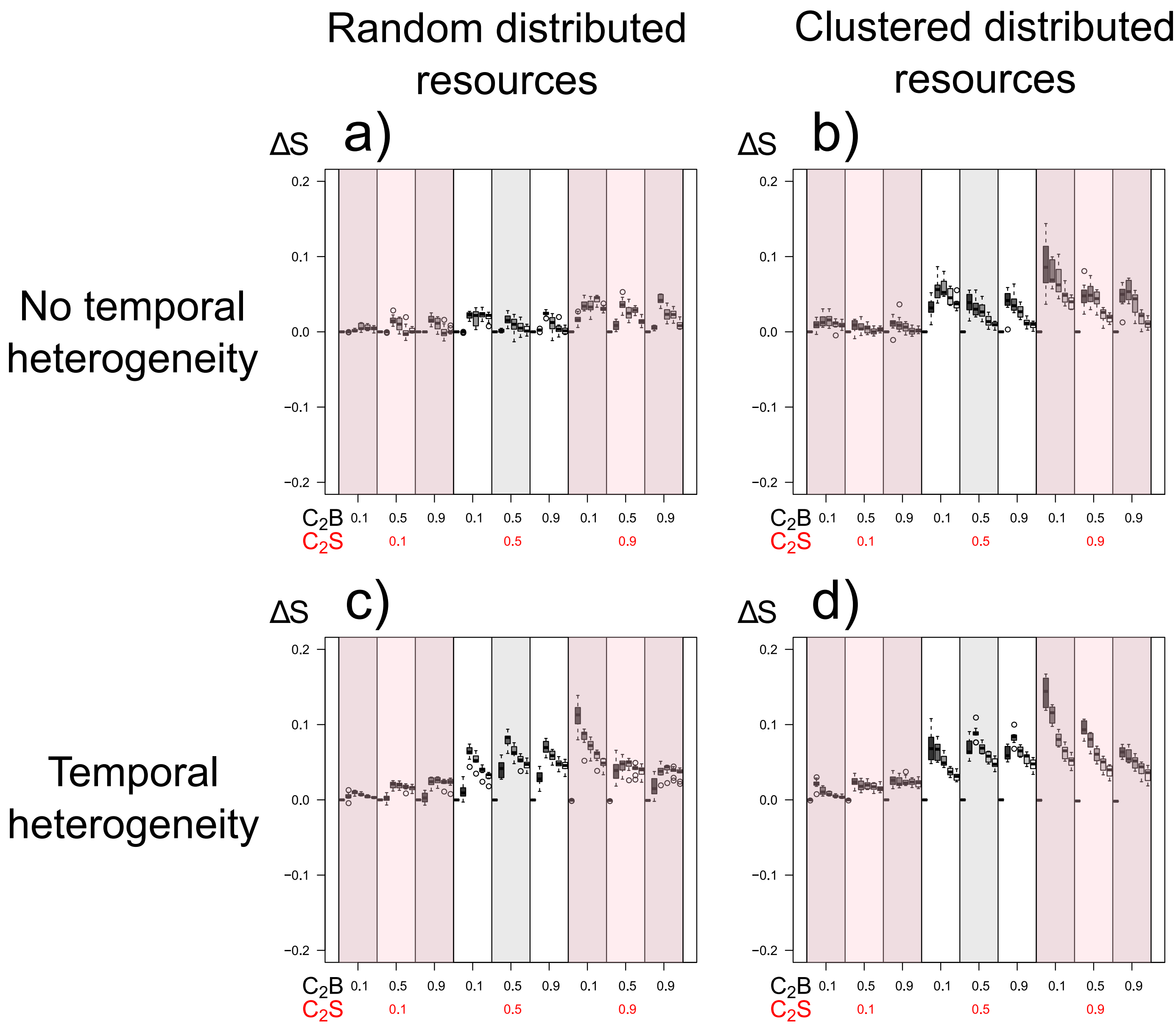


Figure 3: Effects of spatial and temporal resource variability, cooperation behaviour (C_2S ($Coop.$ to $Stock$) and C_2B ($Coop.$ to $Burn$)) and resource diffusion rate (the grey colours in each group of 6 successive box-plots within each colour column represent a variation in dr from 0 (black/left) to 0.5 (whitish/right)) on the difference in mean size of the cooperative agents among the non-cooperation-allowed and the cooperation-allowed simulations (ΔS) for a selected condition of spatial distribution and number of agents (506 individuals with random distribution). Positive values indicate that cooperation promoted an increase in size of the cooperative individuals. The top row (a,b) shows simulation results without temporal resource variability, while the bottom row (c,d) had temporal resource variability. The left columns (a,c) are with a randomized spatial resource while the right columns (b,d) are with two clusters of the resource ("sugarmap").

a larger size of non-cooperative agents than cooperative agents (negative DS). In the other cases of spatial and/or temporal variability of the resource (Fig. 4 b,c,d) the DS was always larger for regularly distributed agents than clustered or randomly distributed agents. Without temporal variation but with spatial heterogeneity of the resource (Fig. 4b), a regular distribution of 506 or 992 agents led cooperative agents to have larger sizes than non-cooperative agents ($DS > 0$). In these cases, an optimum dr value appeared at 0.1. With temporal resource variation (Fig. 4 c-d), a small number of randomly distributed populations of agents had an advantage in cooperating with a dr of 0.2. With 100 agents, the maximum DS at dr of 0.2 was true for all resource distributions. However, the regular distribution of agents still enhanced the advantage of cooperative agents ($DS > 0$).

In term of mechanisms behind these results, the regular distribution of agents allowed optimal sharing of resources in cooperative groups of small size. Indeed, the regular distribution created smaller groups than the two other distribution types (see Appendix E). When comparing the success of growth of cooperative agents to non-cooperative ones, small cooperative groups could do overall better than large groups. Large cooperative groups created some spatial configuration with individuals in the centre of many other, and hence not accessing resources. The intermediate dr values effect was a bit similar: the resource accessibility needed to be high enough but not too high so that all agents could benefits from the resources coming from empty areas.

3.3. Inequality in the cooperation kingdom

Positive changes in the Gini index brought about by cooperation (ΔG, Fig. 5) indicated a more equal distribution of sizes with cooperation than without, among the cooperative agents (and only these agents, see Fig. 2).

Without temporal or spatial resource variation (Fig. 5 a), the variations of ΔG were highly influenced by the dr and spatial distribution of agents. In the cases of random and clustered distribution of agents, cooperation generated a decrease in size equity among cooperative agents for small values of resource

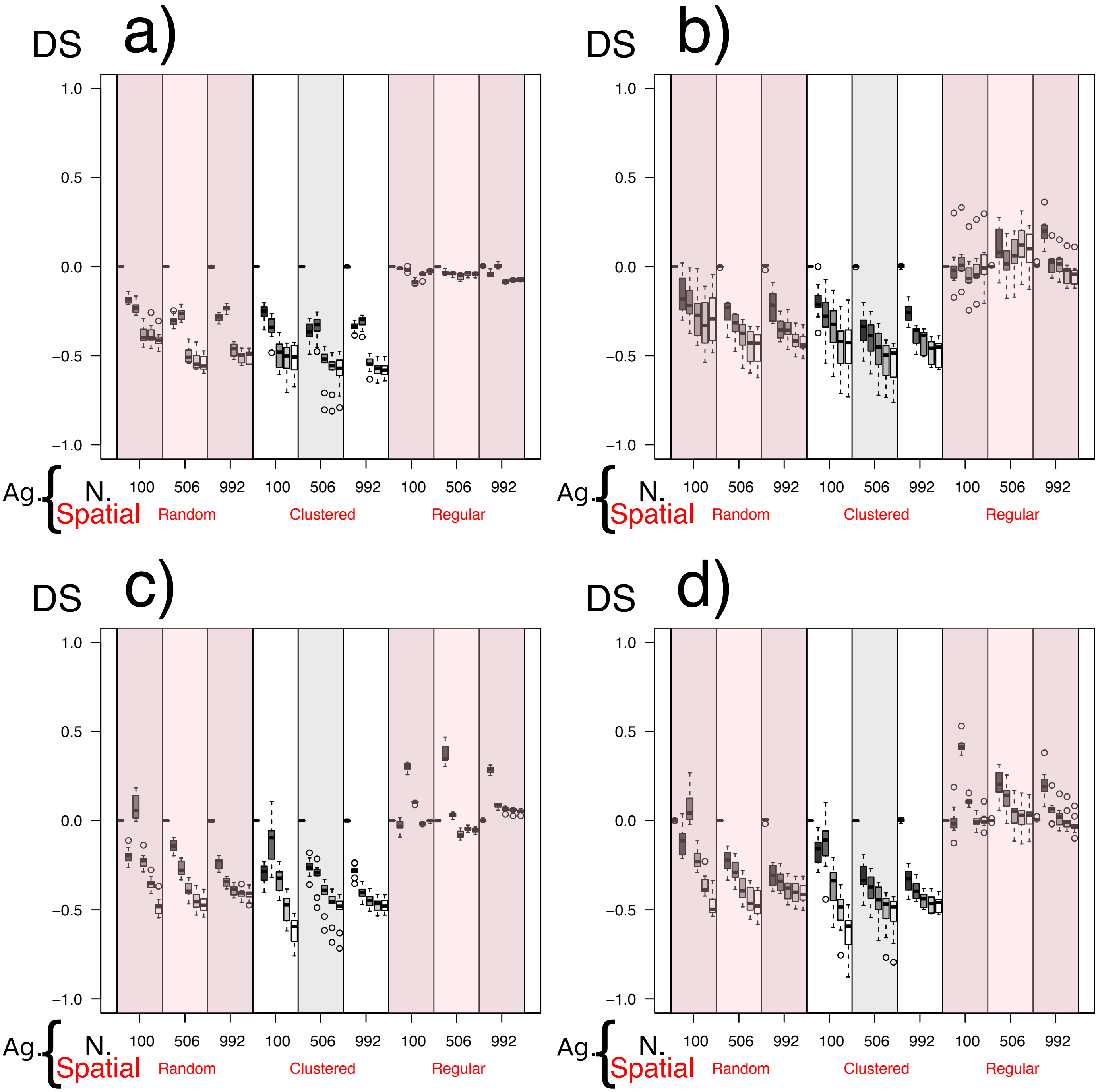


Figure 4: Effects of spatial and temporal resource variability, spatial distribution and number of agents and resource diffusion rate (identical to figure 3) on the difference in mean size between the cooperative agents and the non-cooperative agents (DS) for a selected condition of cooperation behaviour ($C_2S = 0.5$, $C_2B = 0.5$). Positive values indicate that cooperative individuals were larger overall than non-cooperative agents. Graph layout (a-d) is identical to figure 3.

diffusion (when $dr \leq 0.2$, $\Delta G < 0$). This decrease was less visible with only 100 agents. However, high diffusion rates ($dr > 0.3$) led to a small advantage for cooperation in terms of size equity. For these spatial configuration (random and clustered agents) a low resource diffusion dr made that resources were more accessible to border agents of cooperative groups. When dr increases, this advantage disappeared and the groups received more resources, hence the equity increased within the cooperative groups. The regular distribution of few agents (100 or 506) also homogenized the access to resources. With 992 regularly distributed agents, the effect of dr was visible again.

The clustered spatial distribution of the resource (Fig. 5 b) had a decreasing effect on the dispersion of ΔG but also decreased the number of cases with positive ΔG. Clustered resources were not conducive to equity among agents in general, but cooperation increased these inequities in this case (Fig. 5b). Here, the decrease in ΔG was due to a difference of resource access among cooperative agents. The cooperative agents on top of the high resource areas had more resources to share, grow and hence access new resources than the agents in lower resource areas. This created inequity among all the cooperative agents (between groups).

With temporal resource variation, the optimum resource diffusion to obtain a reduction in inequity in the simulations seemed to decrease (comparing Fig. 5 a and c). This was particularly true with 100 individuals. However with 906 individuals, whatever their spatial distribution, inequity was increased with cooperation (Fig. 5c). Adding spatially explicit resource distribution to temporal resource variation did not modify these patterns (Fig. 5d). However, as without temporal variation, a clustered resource was not an opportunity for agents to decrease inequity with cooperation.

We saw previously that cooperation promoted a larger size of cooperators with heterogeneous resource distribution than with homogeneous distribution (Fig. 3 & 4). We see now that these large sizes were built on greater inequity between agents.

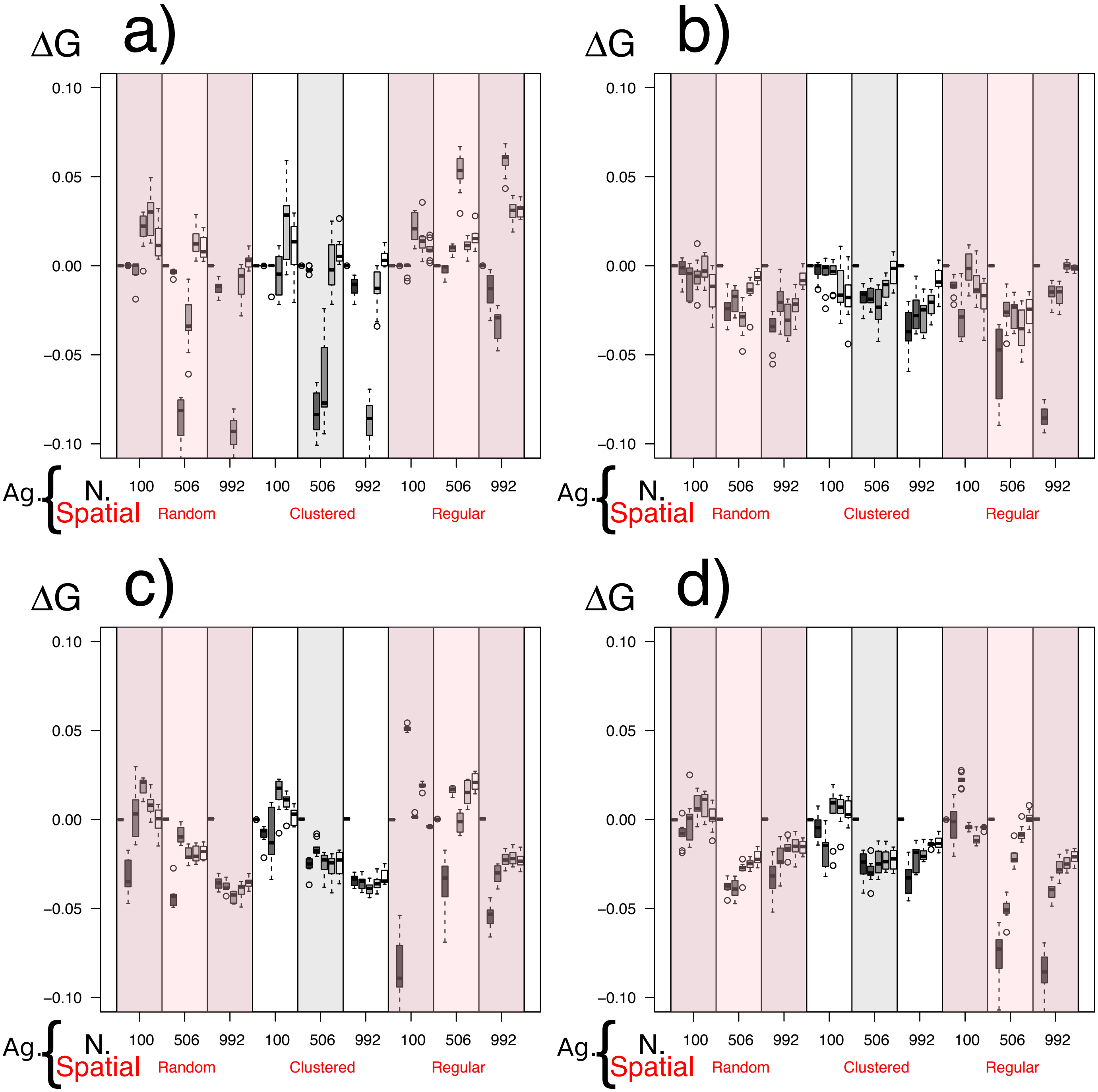


Figure 5: Effects of spatial and temporal resource variability, spatial distribution and number of agents and resource diffusion (identical to figure 3) on the difference in the mean Gini index among the non-cooperation-allowed and the cooperation-allowed simulations (ΔG) for a selected condition of cooperation behaviour ($C_2S = 0.5$, $C_2B = 0.5$). ΔG is computed as the difference of Gini index of sizes of the cooperative agents (only, see Fig. 2). Positive values indicate a more equal distribution of sizes with cooperation than without for the selected agents (that are cooperating when cooperation is allowed). Negative values indicate that inequality increased with cooperation being allowed in the simulations.

3.4. When does it pay to cooperate?

In the results presented above, the simulations were with the same configuration for C_2S (0.5) and C_2B (0.5). It cannot therefore be seen whether agents could use the lever of cooperation rules to reduce inequity. We were interested in finding situations where cooperation was the best solution for agents in terms of a gain in size (ΔS), a larger size for cooperators than non-cooperative agents (DS) and reduced inequity (ΔG). Blank squares in Fig. 6 imply that no configuration with these parametrisations led simultaneously to a larger size with cooperation than without, a larger size of cooperative individuals than non-cooperative individuals and lower inequality among the cooperative individuals when cooperation was allowed. On the contrary, the grey squares indicate a favourable situation for cooperation. For each grey square, Fig. 6 indicates the resource diffusion rate (dr) value(s) that comply with the rule of 75% of simulation results conducive to cooperation for the three indicators.

We can see a clear opposition between simulation without temporal variability (Fig. 6 a-b) and simulation with temporal variability (Fig. 6 c-d) as noted in section 3.1. In the first case, no parametrisations appeared beneficial for cooperation. The second case with temporal variability clearly introduced some positive configurations. However, they were restricted to small numbers of agents (100 or 506) and a regularly spaced distribution of them. In the case with spatial clustering of the resource (Fig. 6d), this was even more strictly confined to the simulations with 100 agents. The regular spatial distribution of agents favours cooperation through two mechanisms: a decrease of spatial competition for resource and the creation of small groups with few connections. These enhance the equity among cooperative agents and hence come out as a major factor in Fig. 6. Lastly, an effect of cooperation rules was also visible. Some cases of C_2S and C_2B did not favour cooperation while others did. More specifically, in the case of a spatially and temporally heterogeneous resource (Fig. 6d), it was good to stock the shared resource a lot (high C_2S) and use it moderately (low C_2B) in order to have beneficial cooperation for a large number of agents.

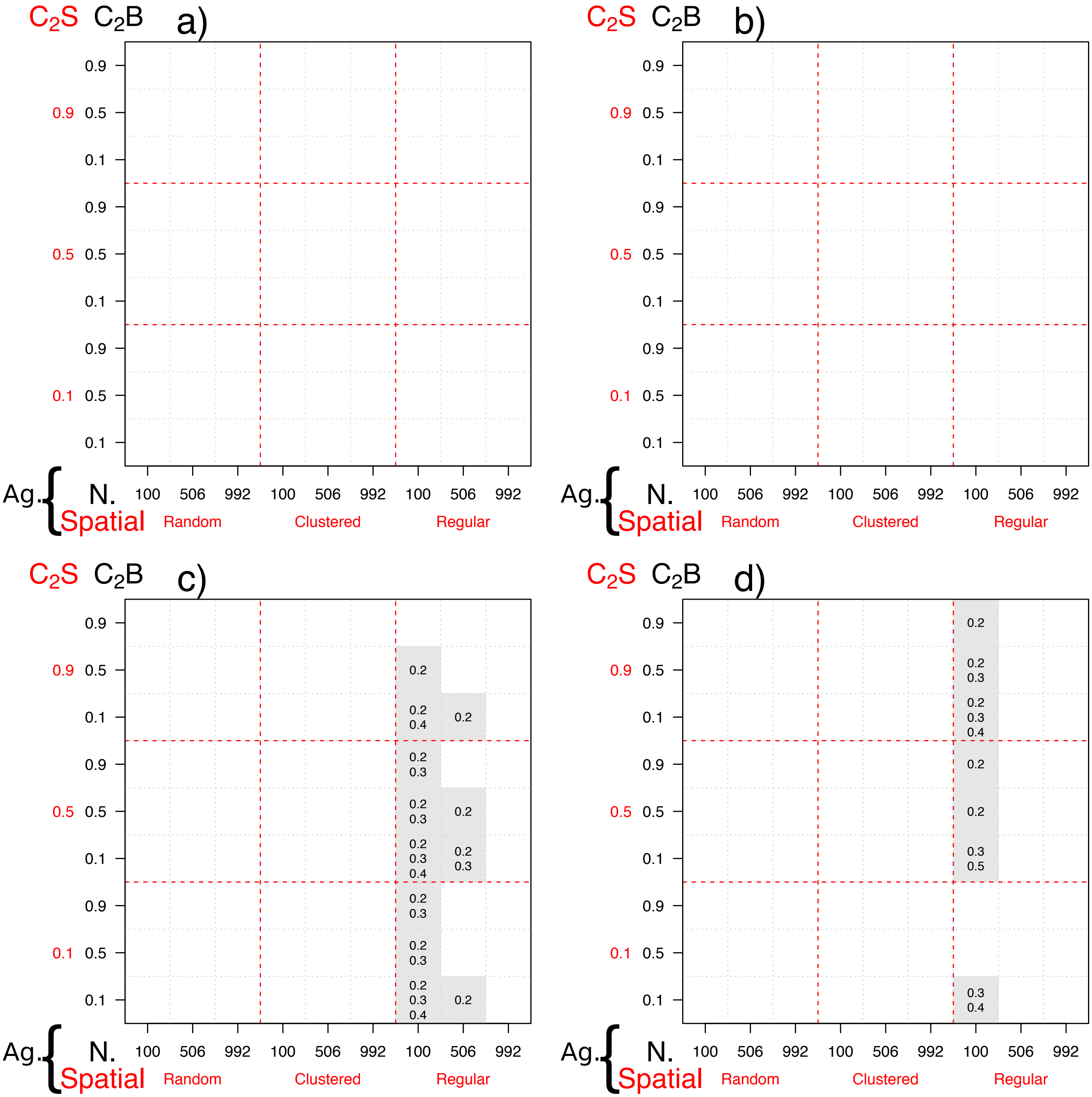


Figure 6: Effects of spatial and temporal resource variability, spatial distribution and number of agents (N. and Spatial) and cooperation behaviour (C_2S and C_2B) on a summary test showing the resource diffusion rate (dr) when all three indicators (ΔS, DS and ΔG) showed a 1st quartile distribution above 0. Blank squares imply that no configuration with this parametrisation led simultaneously to a larger size with cooperation than without, a larger size of cooperative individuals than non-cooperative individuals and lower inequality among the cooperative individuals. The top row (a,b) shows simulation results without temporal resource variability, while the bottom row (c,d) had temporal resource variability. The left-hand columns (a,c) are with a randomized spatial resource while the right-hand columns (b,d) are with two resource clusters ("sugarmap").

4. Discussion

In this paper our objective was double : *i)* support an ontological approach of cooperation compatible with actual consideration on competition, *ii)* illustrate with a model that there may be some conditions when cooperative agents are successful compared to competitive agents. In accordance with previous works (Touza et al., 2013; Pepper and Smuts, 2000; Boza and Scheuring, 2004), our simulations showed that heterogeneity of spatial resources is necessary for the success of cooperation at the group level. We included equity (ΔG) as part of the success of cooperation at the group level to consider potential natural selection on all agents of cooperative groups. In this context, we illustrated that in some settings, temporal scarcity of the resource can have a greater influence over cooperation success than the spatial variability of the resource.

We observed that spatial averaging of resources can be interesting for cooperative agents in the face of scarcity when the diffusion of these resources is not too high. In addition, our model made possible to explore the influence of another dimension in resource heterogeneity: the variability in agent access, especially through their spatial configuration. We observed that the factors favouring equity in access to the resource was conducive to the success of cooperation. So our results illustrate "when does resource scarcity favour group cooperation".

4.1. Configuration of the interactions' topology matters

In a heterogeneous temporal resource context, we found that the regular agent layout concentrated all favourable conditions for cooperation especially for 100 and 506 agents. These results can be interpreted in the light of the rule of Ohtsuki et al. (2006) of a necessary benefit-to-cost ratio above the mean number of interacting neighbours in a network reciprocity configuration. Indeed, our regular spatial configuration of a few agents created a regular lattice in terms of the topological network of interaction. The mean number of interacting neighbours was thus relatively small and the benefits did not need to be as high as in a clustered spatial configuration of agents for cooperation to be more beneficial than individualistic behaviour. Recent work on the topological structure of populations implies that clustered situations could even be, in themselves, never conducive to cooperation (Allen et al., 2017).

We cannot say whether a regular layout is an initial need for cooperation or whether it is the emergent result of local competition like proposed by the "Central place theory" (Christaller, 1933) or the self-thinning rule in ecology (Yoda, 1963; Stoll and Bergius, 2005), but in any event the link between regular spacing and the benefits of cooperation is strengthened by our results. It is thus possible to put forward the hypothesis that it is only when competition is reduced with regular and egalitarian access to the resource that cooperation can be beneficial to all. It would be interesting to investigate empirically the other outputs of the model concerning group size in cooperation. The fact that cooperation is favoured in and beneficial for groups of small numbers of agents should be considered in political policy and particularly in the case of stakeholder empowerment. On the contrary, the current trend in collective irrigation management is to merge small groups to achieve an economy of scale (Delay and Linton, 2019; Campardon et al., 2012). This opposite trend can become critical for maintaining cooperation in large management groups (Axelrod and Keohane, 1985; Allen et al., 2017; Reia and Fontanari, 2017).

Empirical observations by Hamburger et al. (1975) or Smaldino and Lubell (2011) illustrated the role of group size in cooperation. Barnes et al. (2017) questioned cooperation in harvesting common-pool fishery resources considering the fact that fishing is a highly competitive economic activity, in which uncertainty linked to spatial and temporal heterogeneity of the resource is high. In the same way as Ohtsuki et al. (2006), Barnes et al. (2017) used the costs and benefits approach based on resource management. They highlighted in this context some sociological conditions conducive to cooperative behaviour. These interesting observations confirm the theoretical work of Allen et al. (2017) about the limitations of network size and topology on cooperation and illustrate them in the context of a common-pool management system. Our results regarding the number of agents and resource accessibility corroborate these findings. The largest numbers of agents never succeed to obtain cooperation entirely beneficial to cooperative groups in our simulations.

4.2. Temporal scarcity as engine of cooperation

In our model, the sharing capacity of cooperative groups created a temporal buffer for the agents to deal with lack of resources. This explains the important role of temporal scarcity of the resource in favouring cooperation and creating equity within cooperative groups. The temporal variability of the resource necessary for cooperation to be beneficial can also be understood through the benefit-to-cost ratio rule of Ohtsuki et al. (2006) in network reciprocity. In our model, as in many real systems, the costs of setting aside part of the potential resource for harder days to come are temporally immediate. On the other hand, the benefits are temporally worthwhile only if these resources do indeed become scarce at some time. Hence, the benefit-to-cost ratio can favour cooperation at the group level only if those resources are temporally variable. Specific network configurations are necessary for individual benefits of cooperation Allen et al. (2017). But we show that at the group level, the temporal effects of resource availability are important drivers of cooperation, particularly considering the criteria of reducing inequity among cooperative agents (ΔG).

This surprising link between temporal heterogeneity and collective management opens up various avenues of investigation. Indeed, as Springer (2016, 8) says "*[...] any given commons is a geographical matifestation of mutual aid*". Among other things, the possibility of characterizing potential for the emergence of cooperation through some indicators of spatial-temporal variability of resources is an interesting research objective. The theoretical work initiated by Ohtsuki et al. (2006) or Allen et al. (2017) towards characterizing interactions and network configurations lacks the temporal aspects of the resource.

4.3. About our positioning

Among our modelling hypotheses, the nearest neighbour distance used to impose cooperative behaviour between agents (sect. Design concepts 2.2) is a highly structuring hypothesis. This choice corresponds to general beliefs in different research fields. In geography, socio-economics or ecology, cooperation is strongly tied to the spatial proximity of agents (Tobler, 1970). It would be interesting in future work to analyse the effect of a different topology of social networks on the benefits of sharing resources.

Another modelling assumption to explore further is the choice of using one kind and one use of resource. Obviously, real resources and access to them can be complementary between agents, plural and temporally variable (Torre and Wallet, 2014). Our resource-based assumption of relationships among agents was influenced by Epstein and Axtell (1996) and their artificial society where agents eat and metabolize a renewable resource. Our agents' optimum behaviour was resource-oriented. This modelling choice was justified by the simple representation of agent interactions.

Our objective was to illustrate in which cases cooperation was successful compared to competition in some spatial and temporal environments. For a given model or system, once the settings favouring cooperation are identified, it could be possible to explore in these domains and margins if cooperation can emerge in the face of competition. Working on resource-based definitions, one could balance the debate between competition and cooperation in the same terms. This ontological equilibrium between cooperation and competition, without having to rely on "games theory" and "prisoner's dilemma" approaches (Waldeck, 2013; Ohdaira and Takao, 2009; Cohen et al., 2001; Axelrod and Hamilton, 1981) can be seen as the settings for fertile interdisciplinary approaches. Indeed, ecologists as well as social scientists can use our framework to filter their own reality (Varenne, 2017). Hence, this work can be seen as an extension of Epstein and Axtell (1996) focusing on cooperation rather than markets and trade. Models developed considering the resource-based definition of cooperation could also serve to explore spatial pattern formation (Rietkerk and van de Koppel, 2008) in the conditions where cooperation increase the speed of resource exchange among agents compared to the diffusion process (see e.g. for review Kondo and Miura, 2010).

Our model highlights that there are, in general, few circumstances in which cooperation is beneficial. It is worth noting that we gave importance to equity between individuals in our interpretation of beneficial cooperation (through ΔG). In human cooperation, such equity is not always a reality. Indeed, in different cooperative institutions, the equity between individuals is not the objective of the cooperation. The objective is more often a mutual benefit increasing the fitness of each cooperator (Delay, 2015; Gide and Tenin, 2014).

To conclude, our model illustrates that the link between temporal and spatial uncertainty can be understood as a driver leading to the creation of a cooperative group. However, our results do not claim to illustrate how an environmental resource should be sustainably managed, and further studies should explore the emergence of cooperative institutions that manage resources.

5. Acknowledgments

We would like to thank the Limoges University foundation, Engie, and Société Hydro-Electrique du Midi (S.H.E.M.) for their financial support. Simulations were performed on the CBGP HPC computational platform and CALI, the computing cluster at Limoges University, funded by the Limousin region, the European Union, the XLIM, IPAM & GEIST institutes and Limoges University. Thanks go to the CALI team and OpenMole team for their technical support, to two anonymous reviewers and Rebecca Tyson (Associate Editor) who greatly improved the manuscript and to Laurence Dedieu and Peter Biggins for remarks and the English editing of the manuscript.

References

References

Allen, B., Lippner, G., Chen, Y.T., Fotouhi, B., Momeni, N., Yau, S.T., Nowak, M.A., 2017. Evolutionary dynamics on any population structure. Nature 544, 227–230. URL: http://www.nature.com/nature/journal/v544/n7649/abs/nature21723.html, doi:10.1038/nature21723.

Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. Science 211, 1390–1396. URL: http://www.sciencemag.org/content/211/4489/1390.short.

Axelrod, R., Keohane, R.O., 1985. Achieving cooperation under anarchy: Strategies and institutions. World Politics: A Quarterly Journal of International Relations , 226–254URL: http://www.jstor.org/stable/2010357.

Baddeley, A., Rubak, E., Turner, R., 2015. Spatial Point Patterns: Methodology and Applications with R. Chapman and Hall/CRC Press, London. URL: http://www.crcpress.com/Spatial-Point-Patterns-Methodology-and-Applications-with-R/Baddeley-Rubak-Turner/9781482210200/.

Barnes, M.L., Arita, S., Kalberg, K., Leung, P., 2017. When does it pay to cooperate? Strategic information exchange in the harvest of common-pool fishery resources. Ecological Economics 131, 1–11. URL: http://www.sciencedirect.com/science/article/pii/S0921800915306844, doi:10.1016/j.ecolecon.2016.08.005.

Bousquet, F., Duthoit, Y., Proton, H., Le Page, C., Weber, J., 1998. Tragedy of the commons, co-viability of the environment and the society, in: Proceedings of the Third International Conference on Multi-Agent Systems, AAAI Press.

Boza, G., Scheuring, I., 2004. Environmental heterogeneity and the evolution of mutualism. Ecological Complexity 1, 329–339. URL: http://www.sciencedirect.com/science/article/pii/S1476945X04000546, doi:10.1016/j.ecocom.2004.07.002.

Bshary, R., Bergmüller, R., 2008. Distinguishing four fundamental approaches to the evolution of helping. Journal of Evolutionary Biology 21, 405–420. URL: http://onlinelibrary.wiley.com/doi/10.1111/

j.1420-9101.2007.01482.x/abstract, doi:10.1111/j.1420-9101.2007.01482.x.

Campardon, M., Loubier, S., Morardet, S., 2012. L'irrigation en France. Etat des lieux 2010 et évolution. Technical Report PUB00037209. IRSTEA. Montpellier, France. URL: http://cemadoc.irstea.fr/cemoa/PUB00037209.

Christaller, W., 1933. Central Places in Southern Germany. English edition 1966 ed., Prentic-Hall.

Cohen, M.D., Riolo, R.L., Axelrod, R., 2001. The role of social structure in the maintenance of cooperative regimes. Rationality and Society 13, 5–32. URL: http://journals.sagepub.com/doi/abs/10.1177/104346301013001001, doi:10.1177/104346301013001001.

Delay, E., 2015. Réflexions géographiques sur l'usage des systèmes multi-agents dans la compréhension des processus d'évolution des territoires viticoles de fortes pentes : Le cas de la Côte Vermeille et du Val di Cembra. Thèse de doctorat. Université de Limoges. Limoges.

Delay, E., Linton, J., 2019. The exchange of freedom for hydrological certainty and the farmers of the Pyrenees Orientales of France. Environment and Planning C , 1–20URL: https://journals.sagepub.com/doi/10.1177/2399654419838711, doi:10.1177/2399654419838711. aCL.

Edmonds, B., Le Page, C., Bithell, M., Chattoe-Brown, E., Grimm, V., Meyer, R., Montañola Sales, C., Ormerod, P., Root, H., Squazzoni, F., 2019. Different modelling purposes. Journal of Artificial Societies and Social Simulation 22, 6. URL: http://jasss.soc.surrey.ac.uk/22/3/6.html, doi:10.18564/jasss.3993.

Epstein, J.M., Axtell, R., 1996. Growing Artificial Societies: Social Science from the Bottom Up. First edition ed., MIT Press.

Gide, C., Tenin, L.L.e.L., 2014. Économie sociale. Hachette Livre BNF.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecological Modelling 198, 115 – 126. URL: http://www.sciencedirect.com/science/article/pii/S0304380006002043, doi:10.1016/j.ecolmodel.2006.04.023.

Grimm, V., Berger, U., DeAngelis, D., Polhill, J., Giske, J., Railsback, S., 2010. The ODD protocol:A review and first update. Ecological Modelling 221, 2760–2768.

Hamburger, H., Guyer, M., Fox, J., 1975. Group size and cooperation. Journal of Conflict Resolution 19, 503–531. URL: http://jcr.sagepub.com/content/19/3/503.short.

Hamilton, W.D., 1964. The genetical evolution of social behaviour. II. Journal of theoretical biology 7, 17–52. URL: http://www.sciencedirect.com/science/article/pii/0022519364900396.

Hardin, G., 1968. The Tragedy of the Commons. Science 162, 1243–1248. URL: http://www.sciencemag.org/content/162/3859/1243, doi:10.1126/science.162.3859.1243.

Hauert, C., Traulsen, A., Brandt, H., Nowak, M.A., Sigmund, K., 2007. Via Freedom to Coercion: The Emergence of Costly Punishment. Science 316, 1905–1907. URL: http://science.sciencemag.org/content/316/5833/1905, doi:10.1126/science.1141588.

Hijmans, R.J., 2015. raster: Geographic Data Analysis and Modeling. URL: https://CRAN.R-project.org/package=raster. r package version 2.4-20.

Holland, J.N., DeAngelis, D.L., 2010. A consumer—resource approach to the density-dependent population dynamics of mutualism. Ecology 91, 1286–1295. URL: http://www.jstor.org/stable/25661180.

Jeffries, M.J., Lawton, J.H., 1984. Enemy free space and the structure of ecological communities. Biological Journal of the Linnean Society 23, 269–286. URL: https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1095-8312.1984.tb00145.x, doi:10.1111/j.1095-8312.1984.tb00145.x.

Keddy, P.A., 2001. Competition. Population and Community Biology Series 26. 2 ed., Springer Netherlands. URL: http://gen.lib.rus.ec/book/index.php?md5=cdb5b3e6996f5836e80fdb133a9bd6f1.

Kondo, S., Miura, T., 2010. Reaction-diffusion model as a framework for understanding biological pattern formation. Science (New York, N.Y.) 329, 1616–1620. doi:10.1126/science.1179047.

Kropotkin, P.A., 1902. Mutual Aid: A Factor of Evolution. Knopf.

Ohdaira, T., Takao, T., 2009. Cooperation in the Prisoner's Dilemma Game Based on the Second-Best Decision. Journal of Artificial Societies and Social Simulation 12, 7. URL: http://jasss.soc.surrey.ac.uk/12/4/7.html.

Ohtsuki, H., Hauert, C., Lieberman, E., Nowak, M.A., 2006. A simple rule for the evolution of cooperation on graphs and social networks. Nature 441, 502–505. URL: https://www.nature.com/nature/journal/v441/n7092/abs/nature04605.html, doi:10.1038/nature04605.

Ostrom, E., 1990. Governing the commons: The evolution of institutions for collective action. Cambridge university press. URL: http://books.google.com/books?hl=en&lr=&id=4xg6oUobMz4C&oi=fnd&pg=PR11&dq=info:UNqd5tMI_jUJ:scholar.google.com&ots=aN8ouOlDYj&sig=TTmHzigIRcsiuqkbdrGD2nCea4k.

Ostrom, E., Gardner, R., Walker, J., 1994. Rules, games, and common-pool resources. University of Michigan Press.

Pepper, J.W., Smuts, B.B., 2000. The evolution of cooperation in an ecological context: an agent-based model. Dynamics in Human and Primate Societies: Agent-Based Modeling of Social and Spatial Processes , 45–76.

Poteete, A.R., Janssen, M.A., Ostrom, E., 2010. Working together: collective action, the commons, and multiple methods in practice. Princeton University Press. URL: https://books.google.fr/books?hl=fr&lr=&id=5jXmRU7jptsC&oi=fnd&pg=PP2&dq=Ostrom+work+together&ots=zpIV4gSdrs&sig=9Lh6WAakrWCoIehHl4FB_ekpL8w.

Reia, S.M., Fontanari, J.F., 2017. Effect of group organization on the performance of cooperative processes. Ecological Complexity 30, 47–56. URL: http://www.sciencedirect.com/science/article/pii/S1476945X16300733, doi:10.1016/j.ecocom.2016.09.002.

Rietkerk, M., van de Koppel, J., 2008. Regular pattern formation in real ecosystems. Trends in Ecology & Evolution 23, 169–175. URL: http://www.sciencedirect.com/science/article/pii/S0169534708000281, doi:10.1016/j.tree.2007.10.013.

Rogin-Anspach, M., 2002. À charge de revanche: figures élémentaires de la réciprocité. La couleur des idées, Seuil, Paris , France.

Simon, H.A., 1990. A mechanism for social selection and successful altruism. Science 250, 1665–1669.

Smaldino, P.E., Lubell, M., 2011. An Institutional Mechanism for Assortment in an Ecology of Games. PLOS ONE 6, e23019. URL: http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0023019, doi:10.1371/journal.pone.0023019.

Smaldino, P.E., Schank, J.C., McElreath, R., 2013. Increased costs of cooperation help cooperators in the long run. The American Naturalist 181, 451–463. URL: http://www.jstor.org/stable/10.1086/669615.

Springer, S., 2016. The Anarchist Roots of Geography: Toward Spatial Emancipation. 1 ed., University of Minnesota Press, Minneapolis.

Stoll, P., Bergius, E., 2005. Pattern and process: competition causes regular spacing of individuals within plant populations. Journal of Ecology 93, 395–403.

Team, R.C., 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org.

Thiele, J.C., Kurth, W., Grimm, V., 2012. RNETLOGO: an R package for running and exploring individual-based models implemented in NETLOGO. Methods in Ecology and Evolution 3, 480–483. URL: http://onlinelibrary.wiley.com/doi/10.1111/j.2041-210X.2011.00180.x/abstract, doi:10.1111/j.2041-210X.2011.00180.x.

Tobler, W.R., 1970. A computer movie simulating urban growth in the Detroit region. Economic geography 46, 234–240.

Torre, A., Wallet, F., 2014. The role of proximity relations in regional and territorial development processes, in: 54th Congress of the European Regional Science Association, Louvain-la-Neuve: European Regional Science Association (ERSA), St. Petersburg, Russia. URL: https://www.econstor.eu/handle/10419/124376.

Touza, J., Drechsler, M., Smart, J.C., Termansen, M., 2013. Emergence of cooperative behaviours in the management of mobile ecological resources. Environmental modelling & software 45, 52–63.

Varenne, F., 2017. Théories et modèles en sciences humaines: le cas de la géographie. OCLC: 1015308768.

Veldkamp, A., Verburg, P.H., 2004. Modelling land use change and environmental impact. Journal of Environmental Management

72, 1–3. URL: http://www.sciencedirect.com/science/article/pii/S0301479704000684, doi:10.1016/j.jenvman.2004.04.004.

Waldeck, R., 2013. Segregated Cooperation. Journal of Artificial Societies and Social Simulation 16, 14.

West, S.A., Griffin, A.S., Gardner, A., 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. Journal of Evolutionary Biology 20, 415–432. URL: http://onlinelibrary.wiley.com/doi/10.1111/j.1420-9101.2006.01258.x/abstract, doi:10.1111/j.1420-9101.2006.01258.x.

Wilensky, U., 1999. Netlogo. URL: http://ccl.northwestern.edu/netlogo/.

Yoda, K., 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. Journal of Biology Osaka City University 14, 107–129. URL: http://ci.nii.ac.jp/naid/20001449712/.

Appendix A. Visualisation of Submodels

The figure A.1 presents the illustration of the result of equation 3 with different values of gS and depending on the size of the agent (S).

Appendix B. Parameters

We present here the table of the global parameters used in the model.

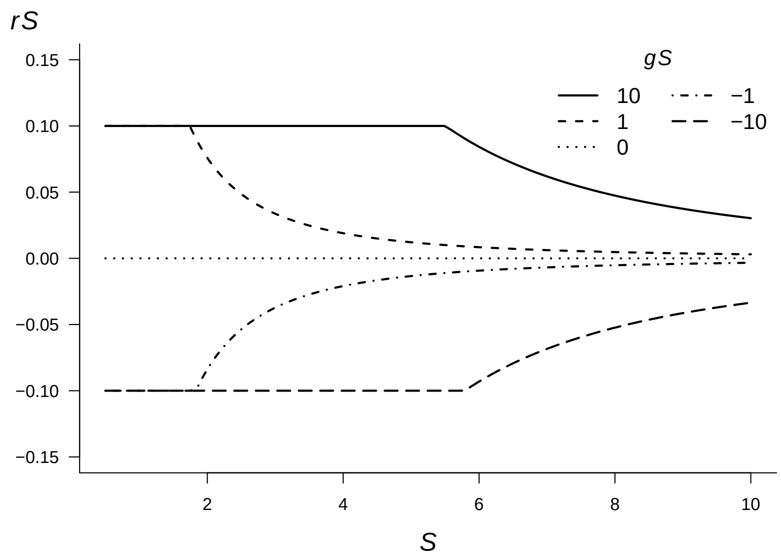


Figure A.1: Illustration of the mathematical function giving growth rate value (rS) depending on agent size (S) and available sugar (gS, or missing sugar when $gS < 0$).

Appendix C. Initialisation of spatial distribution of agents

The positions of agents was always at the centre of a patch. The random distributions of agents was obtained with a Poisson process of complete spatial randomness.

For the creation of 10 different clustered spatial distributions of n agents, we used a Matern Cluster Process of intensity of $\frac{n}{10}$, a radius parameter of the clusters of 0.2 and a number of points per cluster of 10. We kept only simulations of these processes that gave the expected number of agent ($n = 100, 506$ or 992).

For the creation of the regular spacing distributions, we started with an implementation of a hexagonal close packing of the requested n agents. To obtain the 10 different distributions and have agents that could have a minimum neighbour distance below a mean value, we inserted noise around these regular positions. Each agent was then "moved" with a random value of ± 0.5.

Parameter name	Description	Values
dr	Diffusion rate of the resource	0, 0.1, ..., 0.5
Ec	Binary parameter to allow or not the sharing of resources	0 or 1
Tv	Binary parameter to allow or not the seasonal variation of resource replenishment	0 or 1
C_2B	Proportion of the shared resource used by an agent when in cooperation	0.1, 0.5 or 0.9
C_2S	Proportion of available resource allocated by an agent to the shared resource	0.1, 0.5 or 0.9
$maxSz$	Maximum size of agents	10
$minSz$	Minimum size of agents	0.5
$maxR$	Maximum growth rate of agents	0.1
vR	Necessary resource needed for maximum growth	2

Appendix D. Resource visualisation

We present here (Fig. D.2) some examples of resource spatial distribution in different scenarios of diffusion (dr) and with either an initialisation with randomized spatial resource or two resource clusters ("sugarmap"). The spatial distribution of resource is dependant on initialized settings, growth of the agents and diffusion rate. The higher the diffusion rate, the more homogenized the resource.

Appendix E. Network analysis of spatial distributions of agents

We present here (Fig. E.3) some mean characteristics of the cooperative networks (groups of cooperative agents) created in the initialization setting with random, regular or clustered spatial distributions of all agents.

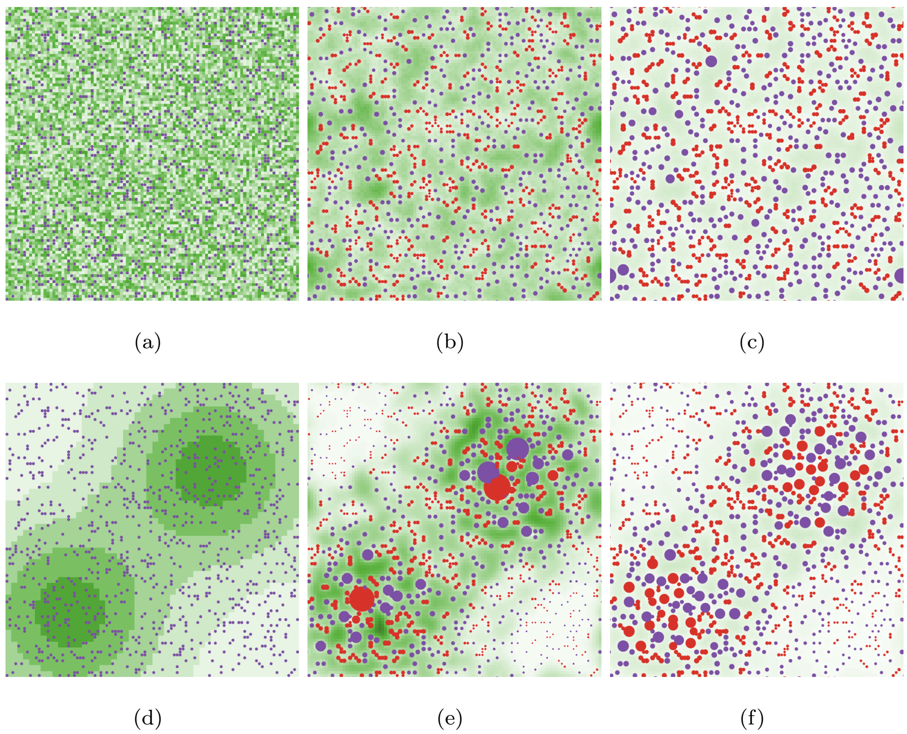


Figure D.2: Evolution of the spatial resource distribution in different scenarios (a): initialized conditions with randomized spatial resource; (b): simulation with $dr = 0.1$ at $t = 1100$; (c): simulation with $dr = 0.5$ at $t = 1100$; (d): initialized conditions with two resource clusters ("sugarmap"); (e): simulation with $dr = 0.1$ at $t = 1100$; (f): simulation with $dr = 0.5$ at $t = 1100$. The red agents are the cooperative agents whereas violet ones do not share resources. All simulations with $Tv = 1$, $C_2B = C_2S = 0.5$ and 992 randomly distributed agents.

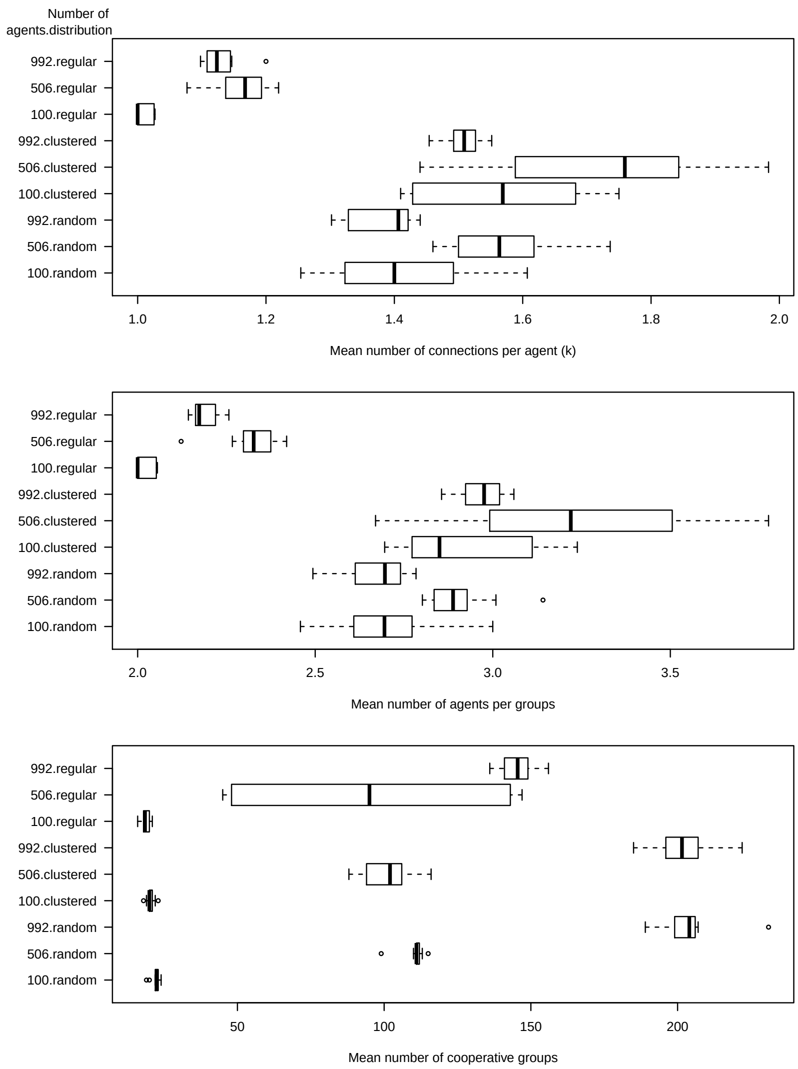


Figure E.3: Mean number of connections, mean number of agents in the networks and mean number of networks of cooperative agents created with the different settings of number and spatial distribution of agents.