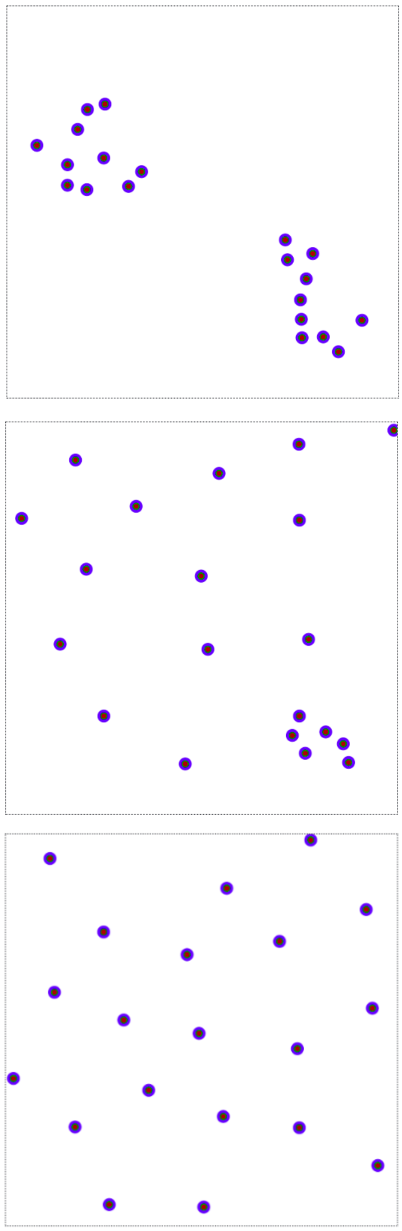
Resource distribution heterogeneity contributes to positive cooperator assortment in a spatial public goods game



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Abstract

The various mechanisms that have been suggested to explain the paradoxical prevalence of cooperation in nature – reciprocal strategies, group selection, kin selection – all presume positive cooperator assortment to some extent: the relatively more frequent interaction of cooperators with other cooperators than with defectors. Such assortment is required for cooperative strategies to be able to compete with mutual defection, which is the Nash equilibrium in public goods and prisoner's dilemma games. We investigate whether resource distribution heterogeneity can contribute to differential assortment prior to such explicit mechanisms, by comparing the levels of cooperator assortment between uniform and clumped resource distributions in a spatial public goods game with minimal and fixed agent behaviour and without evolutionary dynamics. To this end, we utilize an agent-based model in which agents can lose and gain energy by exploiting resources to receive a payoff dependent on whether they are cooperators or defectors. Agents decide to keep exploiting their current resource or to explore for a new one based on a fixed and minimal perspective of their own energy level only. The disparity in timing of these decisions between cooperators and defectors, along with the time it takes to travel to a new resource, contributes to positive cooperator assortment. The results show that clumped resource distribution cause moderately more assortment than uniform resource distributions. This is in line with the Resource Dispersion Hypothesis, which states that a sufficiently rich and dispersed landscape of resources can support group living, and could therefore evolve the type of sociality presumed by cooperative behaviour. However, our results are partially concealed by the presence of excessive "hoarding": the disproportionate accumulation of energy by agents on some resources. Analyses on the differences in quantity and effect of hoarding between resource distributions remain inconclusive. We suggest an improved model in which energy is conserved within the system.

Contents

Abstract 2
Contents 3
Chapter 1: Introduction 5
Chapter 2: Assumptions underlying the model design 7
2.1 Explaining defection via the Resource Dispersion Hypothesis 7
2.2 Minimal and fixed agent perspectives 8
2.3 Energy flow based on resource cooperator proportion 9
2.4 Causal analysis with ABMs 11
Chapter 3: Materials and methods 12
3.1 Model specification 12
3.1.1 Environment properties 12
3.1.2 Agent properties 14
3.2 Simulations 19
3.2.1 Model initialization 19
3.2.2 Run length 19
3.2.3 Iterations 19
3.3 Analysis of model qualities 20
3.3.1 Assortment, clustering, and polarization 20
3.3.2 Hoarding 23
3.4 Sensitivity, robustness, and dispersion analysis 25
3.4.1 Sensitivity analysis 25
3.4.2 Robustness analysis 29
3.4.3 Dispersion analysis 32
3.5 Hypotheses 33
Chapter 4: Results 36
4.1 Main hypothesis 36
4.2 Hypothesis 2 37
4.2.1 Theorem 2a 37
4.2.2 Theorem 2b 39
4.3 Hypothesis 3 39
4.3.1 Theorem 3a 39
4.3.2 Theorem 3b 40
4.4 Hypothesis 4 41
4.4.1 Theorem 4a 41

4.4.2 Theorem 4b 42
4.4.3 Theorem 4c 43
4.5 Hypothesis 5 44
Chapter 5: Discussion 46
5.1 General conclusions 46
5.2 Energy conservation 48
5.3 A fundamental, causal role of accidental buffers 48
5.4 Agent-level energy buffering 49
Bibliography 51

Chapter 1: Introduction

A common way of studying cooperation in nature is using game-theoretic frameworks like the prisoner's dilemma or public goods games (Kuhn, 2024). The dilemma of cooperation is expressed in these frameworks in the form of payoff inequality: in any given game, defectors get more payoff by virtue of paying less cost than cooperators, who should therefore be outcompeted by their more selfish conspecifics. Nevertheless, in the real world cooperation seems to be able to co-exist along with defection. Different ways of "solving" this dilemma have been proposed. The most common solution incorporates repeated games, in which agents can employ different strategies that often focused on kinship or reciprocity (see e.g. Axelrod & Hamilton, 1981). Other solutions also include a network or lattice, across which agents can move to assort themselves with conspecifics (Masuda & Aihara, 2003; Tainaka & Itoh, 2002; Wu et al., 2011; Yamamura et al., 2004; Zhang et al., 2005). Yet others are even more spatially explicit by placing the locations at which games are played *in space* (Burgess et al., 2017; Lanchier, 2019; Tomassini & Antonioni, 2015). Finally, in *ecological* games, the contributing factor is supposed to be *population density* (Funk & Hauert, 2019; Hauert et al., 2006; Wakano et al., 2009; Xu et al., 2011; Zhang & Hui, 2011).

Including a spatial element allows for inquiry into the effect of spatial *heterogeneity* on cooperation. The idea that a heterogenous landscape can facilitate group living is supported by the Resource Dispersion Hypothesis (RDH) (Macdonald & Johnson, 2015). Previous simulation studies have indeed shown an effect of resource distribution heterogeneity on cooperation, although they differ in the way this research question has been modelled (Delay & Piou, 2019; Kun & Dieckmann, 2013; Mosser et al., 2015; Perez & Janssen, 2015; Stilwell et al., 2020). Other models have found a similar effect of resource distribution heterogeneity on cooperation. Delay and Piou's model results suggest a role for resource distribution heterogeneity, but define cooperation as antithetical to competition, rather than to defection (2019). Stilwell et al. show the importance of spatial heterogeneity of resources, but include evolutionary dynamics like selection (2020). Perez and Janssen suggest a small but significant effect of resource distribution heterogeneity on cooperator proportion in the population, but their model includes reproduction and resources that can be exhausted and replenished (2015). Mosser et al. show increased sociality and group territoriality in simulated lions when resources are distributed heterogeneously, but implicitly model kin selection (2015). Kun and Dieckmann show that resource heterogeneity can facilitate cooperation, but model this heterogeneity through differential resource *access* (2013). These models consider cooperation as a dependent variable, but spatial heterogeneity might be a condition that makes cooperation only a possibility, not a fact.

Within this framework of games and payoffs, the key element that allows for the co-existence of cooperators and defectors is *positive assortment*: on average, cooperators get more payoff if they interact relatively more with other cooperators than with defectors (Fletcher & Doebeli, 2008). The idea that assortment mechanisms are key in explaining cooperation is supported by Hamilton's rule, which states that cooperation can evolve when there is sufficient *relatedness* between recipients of benefits (Hamilton, 1964). It has been shown that this relatedness can be interpreted more broadly as positive (spatial) assortment of agents sharing the cooperative behaviour (Fletcher & Doebeli, 2008; Zhang et al., 2010).

Models that study cooperation-defection interaction often either presume positive assortment or choose agent properties whose direct effect is to lead to positive assortment. These properties are then assumed to have been generated by variation and selection in prior evolutionary stages, when positive assortment proved to have survival value. For example, reciprocal strategies like *tit-for-tat*, in which agents copy their game-partner's previous action, contribute to assortment by having agents avoid playing games with defectors (Axelrod & Hamilton, 1981). Another example that more directly assumes positive assortment is group selection, in which groups of agents are selected for based on their collective payoff (Franz et al., 2013; Hermsen, 2022; Pepper & Smuts, 2000).

This thesis investigates the option that positive assortment could emerge *prior* to any assumed agent behaviour or selection. Instead, we hypothesize that the way resources are spread out across space could contribute to assortment. Specifically, we compare uniform to clumped resource distributions. To this end, we design a minimal agent-based model (ABM) in which cooperators and defectors play games and receive payoff (in the form of energy) on resources, and can redistribute themselves, when necessary, across these resources using a random Lévy walk – a common way of modelling agent movement between resources (Nauta et al., 2021; Tomassini & Antonioni, 2015). The research question is whether and how positive assortment can emerge from these minimal agent redistribution dynamics, and whether resource distribution heterogeneity is helpful or even necessary in facilitating this. In particular, we ask whether there is more cooperator assortment in a clumped resource distribution than in a uniform resource distribution.

Cooperative and non-cooperative behaviours are usually assumed to co-evolve under selective pressures (see e.g. Antonioni et al., 2015; Axelrod & Hamilton, 1981; Franz et al., 2013; Hamilton, 1964; Suzuki & Kimura, 2011). One advantage of using an ABM is that it makes it possible to study how this co-evolution can have started with as few assumptions as possible about its prior evolution. In this thesis, cooperation is nothing more than "paying the costs" of resource acquisition, and defection is nothing more than "not paying the costs".

To some extent this thesis addresses a causal question: is positive assortment the result of properties directed to this goal because of selection (as is often assumed), or – vice versa – is positive assortment the accidental result of properties that have been selected for because of other contributions to survival? This thesis researches the second option: our purpose is to investigate whether positive assortment might be facilitated by agents' ability to redistribute themselves across resources based on the payoff they receive, and whether this effect is stronger in a more heterogeneous resource distribution as opposed to a uniform one.

To be able to properly realize this purpose, we make some minimal assumptions that underly the model design, which we address in the next chapter.

Chapter 2: Assumptions underlying the model design

2.1 Explaining defection via the Resource Dispersion Hypothesis

Any agent properties should reasonably be able to be assumed the result of prior evolutionary stages. Following Fletcher and Doebeli, our model includes two types of agents: cooperators, which exploit resources at a certain cost, and defectors, which make use of the spoils of this exploitation without paying the cost themselves (2008; see Chapter 3 for more details). Note that in this form, defectors are merely free-riders, thanking their existence to the cooperators' overproduction, while cooperators are not really cooperating but are just unable or do not need to take control over all the output they produce. We call them cooperators and defectors in the context of the payoff matrices that underly the games they play, without making assumptions about any interactive (cooperative and non-cooperative) behaviours they might be able to portray (more on this in section *2.2 Minimal and fixed agent perspectives*).

Because we deliberately avoid presuming explicit assortment dynamics, the existence of cooperators' overproduction and subsequent defector free-riding must be explained otherwise. We claim that the Resource Dispersion Hypothesis (RDH) can do so. The RDH states that a sufficiently rich and dispersed landscape of resources can support group living at little to no individual cost, without any explicit benefits to cohabitation (like collective hunting, alloparental care, etc.) (Macdonald & Johnson, 2015). The idea is that if any given food source has an uncertain (low) probability of providing enough food for an individual, said individual will need to secure more than one food source to be sure of its survival. Any additional availability of food that may result from this can then be taken advantage of by others. Empirical evidence for this is ubiquitous in nature (see Macdonald & Johnson, 2015 for a table of examples found in the literature).

An example that illustrates this involves the throwing of dice (Macdonald & Johnson, 2015). Suppose that one throw of a die determines the food availability for one resource, for one day, and that only throwing a six provides enough food for one individual. Assuming an even-sided die, the probability of one resource providing sufficient food for one individual, for one day, is $\frac{1}{6} \approx 0.167$. To increase its chances of survival, one individual might therefore attempt to secure multiple resources. For example, with 9 resources – 9 dice – an individual now has a probability of $1 - (\frac{5}{6})^9 \approx 0.806$ of throwing at least 1 six. Because one individual's need for high food security means it will often throw more than 1 six, others can exploit these extra sixes without having to pay the cost of securing the resources themselves.

Although the assumption in our model is that cooperators' exploits are fully converted into payoff for all agents present at a resource, the RDH can nevertheless explain the existence of free-riders as having evolved in moments of food abundance, taking advantage of the additional effort solo exploiters made to be certain of having enough food availability for the day. This is in line with the way cooperators (solo exploiters) and defectors (free-riders) are defined in our model. Having to share its exploits is then not a failure of a cooperator, but merely a property that developed in the face of foraging uncertainty.

More generally, the RDH explains how in situations with a patchy resource distribution, multiple individuals can share patches as long as they can all acquire what they need and their presence does not cost each other (Macdonald & Johnson, 2015). This *may* or *may not* result in the evolution of sociality. Jones et al. call this role of the environment in supporting sociality an "ecological scaffold" (2023). Once this scaffold is taken away, whatever form of sociality had evolved need not disappear. Group living may then endure for functional rather than accidental reasons. Resource distribution heterogeneity may in itself be able to contribute to the endurance of sociality by allowing solo exploiters to assort themselves away from free-riders.

Note that the patchy resource distribution (over space or time) that the RDH is referring to should be distinguished from the resource distribution heterogeneity in this thesis. The patchiness in the RDH is merely the cause of the uncertainty of the foraging attempts, by making agents visit multiple food sources to ensure their survival. In our model, each individual resource is capable of feeding every visiting cooperator with certainty, unless too many defectors are present. The heterogeneity in the distribution of resources is only relevant insofar it facilitates positive assortment. One resource in our model should therefore be seen as having the implied patchiness the RDH is referring to, consisting of multiple food sources whose exploitation by cooperators allow for defectors (free-riders) to cohabitate the resource. The crucial claim of the RDH then, is not what counts as a resource, but that necessary over-exploitation (by agents we call cooperators) due to environmental uncertainty allows for the appearance of free-riders (agents we call defectors), which in turn increases the uncertainty of the over-exploiters' foraging attempts.

However, the RDH is not causal and does not refer to a specific dynamic of group forming, nor of group living. It merely states that resource dispersion (uncertainty) can play a "facilitating, rather than a determining, factor leading to group formation" (Macdonald and Johnson, 2015). Group formation as a result of this facilitation could then be the cause as well as the result of any interactive (cooperative and non-cooperative) behaviours of agents, but that is a step beyond this thesis. All we are interested in, is the role of resource distribution heterogeneity in the generation of positive assortment of cooperators.

Aside from the cooperative and free-riding behaviour, our model requires some form of cooperator and defector travel or exploration, a form that assumes as little as possible about the agents' individual perspective on their received payoff due to prior evolution. On its own, the RDH does not definitively state that individuals *will* live in groups, just that it creates the opportunity to (Macdonald & Johnson, 2015). In the next section, we expound on these minimal agent perspectives.

2.2 Minimal and fixed agent perspectives

As the purpose of this thesis is to study positive assortment as a result of resource distribution heterogeneity, not of direct interactive (cooperative or non-cooperative) behaviours, decisions to leave a resource, travel, and find a new one, should be as simple as possible and based only on an agent's limited individual perspective. As mentioned in section *2.1 Explaining defection via the Resource Dispersion Hypothesis*, the cooperators and defectors in our model have no direct interaction with each other, but only with the resource they occupy. In the perspective of either type of agent, the presence of the other type at the resource changes its properties – namely, the payoff it provides. When the amount of defectors increases at a resource, the same amount of foraged output is shared across a larger number of agents, meaning a lower share for each individual agent. This results in agents making the decision to leave and try foraging at resources elsewhere.

This view of cooperation and defection is slightly different from the one that is commonly taken in the literature (Delay & Piou, 2019). Cooperation as defined as an act providing a direct benefit to a recipient – an *inter*action – implies a more complex agent perspective, one where agents must be aware of other agents and their actions. For example, the idea of public goods games where the gains of a group's foraging efforts are greater than the sum of the individuals' efforts, follows this line of though (see e.g. Hauert et al., 2006). But competition itself – in the sense of being forced to share common resources – is not necessarily interactive in that sense. The cooperators in our model never acquire more resources collectively than they would on their own: they are merely in competition with defectors who make use of their efforts. A better definition of cooperation is therefore one where the benefit that an agent's (foraging) act provides is experienced by the other through its own action on the resource (Delay & Piou, 2019). In other words, a defector's experience of a cooperator's beneficial foraging attempt is mediated through the resource.

The point of this more minimal definition of cooperation is that in studying the effects of resource distribution heterogeneity on positive assortment, we do not want to include any unnecessary assumptions about agent behaviours or perspectives that might directly *influence* this assortment, or that have to be assumed to be *caused by* assortment.

In the above view, cooperators and defectors are selected for based on their payoff, rather than their interactive behaviour. That is why assortment is necessary: it is the only way in which the payoff of cooperators will change relative to that of defectors (Fletcher & Doebeli, 2008). Note that in our model, the selective process is completely absent. Besides being elementary, the cooperator and defector properties are also fixed. There are no evolutionary cycles with agent variation and selection. If assortment does not happen due to selection, then travel – in the sense of redistribution of cooperators and defectors across the resources – is the only form of assortment.

As stated, this agent redistribution across resources is only a consequence of the payoff they receive. Neither type of agent has an overview of other agents, nor of resources' locations and conditions. When leaving a resource, agents travel at random (using a Lévy walk) until they come across a new resource, where again their decision to stay or leave is fully dependent on the received payoff. This "blind" exploration as a result of limited individual agent experience, is the only form of group formation present in our model. There is no evolutionary process selecting against poorly performing agents, and reproducing adequately performing ones. In the worst case, poorly performing agents simply die. This allows us to better isolate the causal effect of resource distribution heterogeneity on assortment.

Agent redistribution is thus the consequence of two key elements: travel *time* and *timing*. The former is influenced by the resource distribution, while the latter is influenced by the interplay between the payoff system and agent distribution. This interplay requires some assumptions about *how* agents base their decision to leave a resource and explore on their payoff. The next section explains how and why these decisions are based on agent *energy*, and how this energy flows through the system.

2.3 Energy flow based on resource cooperator proportion

Energy, in the form of accumulated payoff, is a necessary core concept in the design of our model. It is what makes up an agent's limited individual perspective. Would this perspective merely be based on current payoff, rather than accumulated payoff, the redistribution dynamics would happen too quickly, and there would be no time for agents to assort themselves. As stated in section *2.2 Minimal and fixed agent perspectives*, travel time and timing are key concepts in our model, and without buffered energy, that importance is diminished.

Each agent starts out with the same amount of energy. At resources, they lose energy at a fixed rate (due to their metabolism), and gain energy through payoff. At any resource, this payoff is lower for cooperators than for defectors, because cooperators pay the cost of exploitation, while defectors make use of what is foraged by the cooperators.

Whether an agent's energy increases or decreases, then, depends on whether their payoff is high enough. This payoff is in turn dependent on the proportion of cooperators present at the resource. The dynamics of our model can therefore be viewed as a flow of energy through the components of the model: the resources and agents. In this view, both the resources and the agents are energy buffers – the agents because they require a constant intake of energy to be able to survive, and the resources by virtue of having agents cohabitating them.

As mobile agents, cooperators and defectors can only survive by being able to leave resources with insufficient payoff. This requirement implies that agents should be able to decide whether they are better of staying at their current resource, or trying their luck at another one. Travel takes time, and in this time, agents' cannot buffer energy, potentially falling behind their conspecifics.

Using energy as the perspective that agents base their decisions on, allows for a clearer definition of defectors and cooperators. Resources supply energy to be exploited by cooperators, while in the perspective of the defectors, the cooperators at the shared resource are the suppliers of energy. Given enough defectors, cooperators start losing more energy than they gain, eventually causing them to make the decision to leave their resource when their energy gets below a certain threshold. This way, defectors lose their own source of energy (the cooperators), which implies that it is reasonable to assume that prior evolution has limited the relative number of defectors to an amount that is compatible with the survival of the cooperators.

In this design, energy flows into the system from the resources. This inflow is limited only by the number of cooperators currently exploiting the resources. It might make sense to limit this further, for example in a way that keeps the energy in the system somewhat constant, but that would mean the temporary depletion of some resources. This would interfere with our research question: the effect of the resource distribution heterogeneity on positive assortment. A resource without energy would not be a resource from the perspective of the cooperators, and thus resource distribution heterogeneity would vary across time, rather than just across model runs.

The pragmatic alternative is therefore to assume that no resource can ever be depleted. Then cooperators only have to leave because of the arrival of too many defectors, which lowers the cooperator proportion to such an extent that the cooperators' increase in energy becomes lower than their metabolism requires, which eventually causes their energy to dip below the threshold which makes them leave the resource. Energy only ever truly leaves the system through the agents' metabolism, and is otherwise redistributed among agents, causing the assortment dynamics we are interested in studying. Proper tuning of the model implies limiting the inflow of energy by setting the payoff that resources can grant cooperators low enough so that they do not gain too much energy and remain stationary, but high enough so that they have the opportunity to buffer energy and use this to stabilize their assortment with other cooperators – see section *3.4.1 Sensitivity analysis* for an explanation of this. This differentiates travel timing between agent types in such a way that it results in the assortment dynamics we are interested in studying.

Although our model does not realize the ideal of equal inflow to outflow of energy, it is nevertheless minimal by making travel *time* and travel *timing* (as based on cooperator proportion) the sole parameters of the assortment dynamics. By design, travel timing differs between agent types to cause assortment dynamics. Travel time between resources is varied through the use of different resource distributions, in which way we can measure to what extent this steers the assortment dynamics in the direction of positive cooperator assortment.

2.4 Causal analysis with ABMs

The timing of events like an agent's decision to leave a resource implies a causal sequence. The advantage of using an ABM is that we can control this sequence in detail. If we want to use ABMs as a tool for causal analysis, we should therefore first of all get this sequence right (Manzo, 2022b). As in any model, the input – including the random seed used – completely determines the output. This means that if there is a surprising emergent property, the cause of it must be hidden in the initial setup of properties and behaviours of the agents and their environment, plus the effect of any stochasticity. A causal interpretation of the dynamics of our ABM therefore requires that the input (the initial setup) can reasonably be thought of as the result of prior evolution, and is not in any sense dependent on the emergent output of the ABM. The assumptions we have discussed in this chapter are intended to support this.

If we are to study positive assortment as emergent output, it means that whatever properties our agents have, they cannot be thought of as the result of positive assortment themselves. Having defined cooperators merely as agents with the willingness to incur a cost to be able to exploit a resource, and defectors as agents taking advantage of the abundance of food exploited by cooperators, our cooperator and defector properties make no reference to direct interaction with other agents, and can be assumed to have evolved as a consequence of the RDH, rather than of positive assortment.

This ABM was first tuned using a uniform resource distribution, to find an initial setup that leads to some assortment pattern as a consequence of the differential travel timing between agent types, as well as the stochasticity in the ABM as present in the random travel (time and path). That assortment pattern can be said to be new and emergent. Resource distribution heterogeneity alone – without random travel or disparity in travel timing between agent types – cannot generate the agent redistribution dynamics that lead to positive assortment. As such, the assumptions discussed in this chapter are meant to inform the minimal dynamics that can lead to some assortment pattern. Only then can we properly establish the causal effect of resource distribution heterogeneity on positive assortment.

Chapter 3: Materials and methods

The model was created in the Python library *Mesa* (Kazil et al., 2020). The main body of code was written in Python 3, and the visualization was done using JavaScript (Van Rossum & Drake Jr, 1995). In this chapter, we provide a description of the model, an analysis of its behaviour and emergent properties, and the hypotheses which we test to answer the research question.

3.1 Model specification

3.1.1 Environment properties

3.1.1.1 Environment parameters

Table 1. List of environment parameters with their default value and possible values when used in an analysis.

Parameter	Description	Default value
$\boldsymbol{A}$	Surface area (in squared distance units)	1000
$\boldsymbol{R}$	Resource distribution	“Uniform” (RU)
$\boldsymbol{M}$	Number of resources	20
$\boldsymbol{N}$	Initial number of agents	200
$\boldsymbol{k}$	Initial cooperator proportion	0.8
$\boldsymbol{b}$	Exploitation benefit	2
$\boldsymbol{c}$	Exploitation cost	0.5

3.1.1.2 Resource distributions

The model consists of a toroidal landscape of $A = 1000\ m^2$ (Table 1), visualized as a square width equal width and height $\sqrt{1000}\ m$, where m denotes the basic distance unit. Resources are placed in this landscape using a *Lévy dust* process, in which each resource is placed along the path of a Lévy flight (Nauta et al., 2022). First, a random location is chosen for the initial resource. Second, the distance d between subsequent resource placements is sampled from a truncated Pareto distribution:

$$\Pr(d) = \begin{cases} d^{-\gamma} & if\ d_L \leq d < d_U \\ 0 & otherwise \end{cases}$$

where γ is the Lévy shape parameter, d_L the lower bound, and d_U the upper bound. In our $1000\ m^2$ landscape, $d_U = 20\sqrt{5}\ m$, the length of the diagonal of the square world. d_L differs depending on the intended resource distribution, and also determines the minimum distance between any two resources.

Third, the orientation angle o (in radians) between subsequent resource placements is sampled from a uniform distribution:

$$\Pr(o) = \begin{cases} \frac{1}{2\pi - 0} & if\ 0 \leq o \leq 2\pi \\ 0 & otherwise \end{cases}$$

The combination of the Lévy shape parameter γ and minimum resource distance d_L characterizes different levels of resource heterogeneity. In our analyses, we use the following combinations and resulting distributions **RC** (“clumped”), **RCU** (“clump-in-uniform”) and **RU** (“uniform”) (Figure 1):

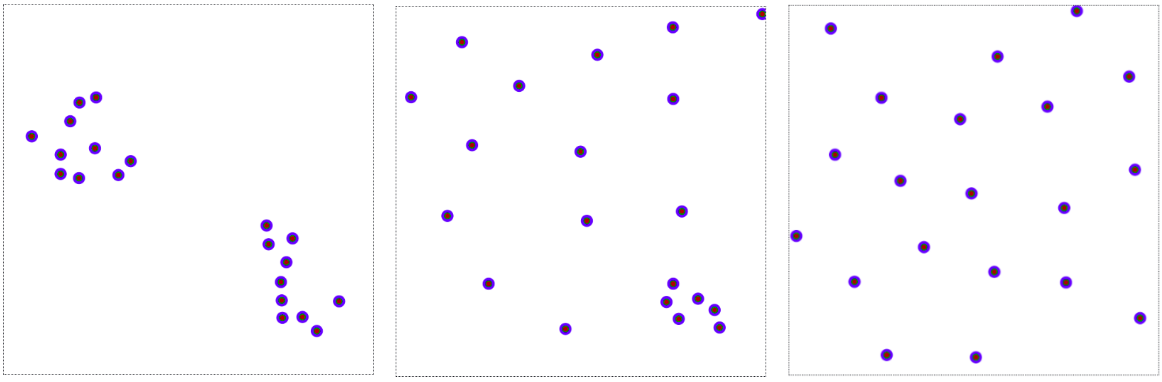

Figure 1. A "clumped" resource distribution RC (left) with $\gamma = 2.0$ and $d_L = 1.5$, a "clump-in-uniform" resource distribution RCU (middle) with $\gamma = 2.5$ and $d_L = 1.5$, and a "uniform" resource distribution RU (right) with $\gamma = 3.0$ and $d_L = 6.0$. Note that each distribution has $M = 20$ resources, and a resource (blue dot) is visualized with the diameter of one distance unit.

The main goal is to compare the clumped to the uniform distribution, but the clump-in-uniform distribution is used to check whether it is the presence of a clump, rather than clumpiness overall that has the largest influence on the model.

Following Dry et al. (2012), for a set of resources R we calculate a clustering measure $ResClust(R) = \frac{r_o(R)}{r_e(R)}$ as the observed divided by the expected mean nearest resource distance, where

$$r_o(R) = \frac{1}{|R|} \sum_{i \neq j}^{|R|} \min{(d_{ij})}$$

$$r_e(R) = \frac{1}{2} \sqrt{\frac{A}{|R|}}$$

with $|R| = M = 20$ the cardinality of set R, $A = 1000$ the surface area of the landscape (Table 1), and d_{ij} the distance between resource i and j. The expected mean nearest resource distance $r_e(R)$ is based on the assumption that resource locations are independently chosen from a uniform distribution of all possible points, meaning a clustering measure of 1 means random resource placement, $\ll 1$ a clustered resource placement, and $\gg 1$ a uniform resource placement (Dry et al., 2012). The maximum value equals 2.149, as in a hexagonal lattice.

For the three resource distributions in Figure 1, we calculate clustering measures of $ResClust(RC) = 0.52$ for the clumped distribution, $ResClust(RCU) = 1.40$ for the clump-in-uniform distribution, and $ResClust(RU) = 1.78$ for the uniform distribution.

3.1.1.3 Resource qualities

Each resource has the same fixed exploitation benefit $b = 2$ and cost $c = 0.5$, and cannot be depleted (Table 1). At model initialization, resources are placed according to the distributions in Figure 1, and do not move or disappear during the model run.

3.1.1.4 Agent population

Let:

- $Cnum_{tot}(t)$ and $Dnum_{tot}(t)$ be the total number of cooperators and defectors, respectively, at timestep t
- $Cprop_{tot}(t) = \frac{Cnum_{tot}(t)}{Cnum_{tot}(t)+Dnum_{tot}(t)}$ be the total proportion of cooperators at timestep t

At model initialization ($t = 0$), the agent population consists of 200 agents, with

$$Cprop_{tot}(0) = k = 0.8$$

$$Cnum_{tot}(0) = k * N = 160$$

$$Dnum_{tot}(0) = N - (k * N) = 40$$

3.1.2 Agent properties

3.1.2.1 Agent parameters

Table 2. List of agent parameters with their default value and possible values when used in the analysis.

Parameter	Description	Default value
$\boldsymbol{E_{init}}$	Initial agent energy	40
$\boldsymbol{E_{loss}}$	Energy loss per timestep when exploiting	1.2
$\boldsymbol{E_{thresh}}$	Energy threshold below which exploiting agents become unhappy, potentially switching to exploration	50
$\boldsymbol{P_{explore}}$	Initial probability of exploration when unhappy agents' energy first gets $< E_{thresh}$	0.1
$\boldsymbol{P_{incr}}$	Increase in probability of exploration for each additional timestep that energy $< E_{thresh}$	0.01
$\boldsymbol{P_{coop}}$	Probability of unhappy defectors to temporarily cooperate instead of explore	0.5
$\boldsymbol{T_{averse}}$	Multiplication factor to determine how many times the average energy of the last travels is required for unhappy agents to start exploring (risk aversity)	1
$\boldsymbol{T_{memory}}$	The number of previous travels taken into account when determining how much energy is required to travel to a new resource	1
$\boldsymbol{B}$	Number of timesteps exploring agents spent on a close Lévy walk with shape parameter γ_c instead of γ_f	10

γ_c	Lévy shape parameter for close searches	3
γ_f	Lévy shape parameter for far searches	2
s	Step length	1
rad	Detection radius	1

3.1.2.2 Exploitation

Agents can be in one of two modes: *exploitation* (foraging on a resource) or *exploration* (travelling to a new resource). When exploiting, agents can be either *happy* or *unhappy*. There are two types of agents, *cooperators* and *defectors*, which differ in the way they exploit, but not in the way they explore.

At model initialization, agents start out happy and exploiting on a random resource, with energy $E(r, t = 0) = E_{init} = 40$ for all resources $r \in R$. At each timestep they exploit, they lose energy of $E_{loss} = 1.2$ (Table 2). Simultaneously, they gain energy through *payoff* as determined by a basic public goods game (Fletcher & Doebeli, 2008). Let:

- $Cnum(r, t)$ and $Dnum(r, t)$ be the number of exploiting cooperators and defectors at resource r at timestep t, respectively
- $Cprop(r, t) := \frac{Cnum(r,t)}{Cnum(r,t)+Dnum(r,t)}$ be the cooperator proportion at resource r and timestep t

Then cooperator and defector payoff are given by

$$Cpayoff(r, t) := Cprop(r, t) * b - c$$

$$Dpayoff(r, t) := Cprop(r, t) * b$$

where b and c denote the benefit and cost of a resource (Table 1). In other words, defectors defect by not paying the cost of exploitation c. At their default values $b = 2$ and $c = 0.5$, the cost is 25% of the benefit. With an initial total cooperator proportion $k = 0.8$, we can calculate the cooperator and defector payoff at uniform agent distribution as a simplified average:

$$Cpayoff_{avg}(t, R) \approx 0.8 * 2 - 0.5 = 1.1$$

$$Dpayoff_{avg}(t, R) \approx 0.8 * 2 = 1.6$$

Note that by design, $Cpayoff_{avg}(t, R) < E_{loss}$ and $Dpayoff_{avg}(t, R) > E_{loss}$, meaning cooperators lose energy and defectors gain energy on average. If both cooperators and defectors gained energy on average, all agents would stay on their resource and keep gaining energy indefinitely. If both cooperators and defectors lost energy on average, no agent would stay on a resource for long and we would not be able to measure any assortment. The choice for the proportion between average cooperator energy change per timestep $Cpayoff_{avg}(t, R) - E_{loss} = -0.1$ and average defector energy change per timestep $Dpayoff_{avg}(t, R) - E_{loss} = 0.4$ is to allow for assortment without too much loss or gain of energy of either agent type (see section *3.4.1 Sensitivity analysis* for a more in-depth discussion).

At each timestep t and resource r, an exploiting agent's energy $E(r, t)$ is updated as

$$E(r, t) = E(r, t - 1) + payoff(r, t) - E_{loss}$$

where $payoff(r, t) = \begin{cases} Cpayoff(r, t) \text{ } if \text{ } cooperating \\ Dpayoff(r, t) \quad if \text{ } defecting \end{cases}$

When $E(r,t) < E(r,t-1)$ and $E(r,t) < E_{thresh} = 50$, exploiting agents become *unhappy* (Table 2). Note that the second condition is satisfied at model initialization because $E_{init} < E_{thresh}$, which forces assortment to take place immediately. When still exploiting and $E(r,t) \geq E(r,t-1)$ or $E(r,t) \geq E_{thresh}$, agents become happy again and continue exploiting.

At each timestep agents are unhappy, they can start exploring with a certain probability

$$\Pr(explore) = P_{explore} + P_{incr} * t_{unhappy}$$

where $P_{explore}$ is the initial probability of exploration, P_{incr} is the probability increase at each timestep, and $t_{unhappy}$ is the number of previous consecutive timesteps they have been unhappy (Table 2).

Rather than exploring, defectors can instead temporarily start cooperating with probability P_{coop} (Table 2). They will then count as a cooperator and receive a corresponding payoff until $E(r,t) < E(r,t-1)$ or $E(r,t) \geq E_{thresh}$, when they will revert back to being a defector. This allows defectors to exploit a resource even when not in the presence of cooperators, without making assumptions about their capacity to detect what (type of) agents are on the resource (see section *3.4.2.3 Defectors' ability to cooperate*).

To prevent agents from exploring when they do not have the energy to do so, agents do not leave their resource when their energy is too low, specifically when

$$E(r,t) < AvgTravelE\left(T_{memory}\right) * T_{averse}$$

where $AvgTravelE\left(T_{memory}\right)$ is the average energy spent during a maximum of T_{memory} previous travels, and T_{averse} is a multiplication factor that determines how risk averse agents are (Table 2).

When agents nevertheless run out of energy, they are removed from the model. See sections *3.4.1 Sensitivity analysis*, *3.4.2.2 Agent death* and *5.1 General conclusions* for further discussion on this design choice.

3.1.2.3 Exploration

In exploration mode, agents first search for new resources within a detection radius rad of 1 distance unit (Table 2). If there are resources within this detection radius other than the last resource they visited, agents go to the closest of those resources. If not, agents start moving around the landscape according to a Lévy walk (James et al., 2011). Specifically, they first sample a heading h from a uniform distribution:

$$\Pr(h) = \begin{cases} \dfrac{1}{2\pi - 0} & if\ 0 \leq h \leq 2\pi \\ 0 & otherwise \end{cases}$$

Then, they sample a distance d from a truncated Pareto distribution:

$$\Pr(d) = \begin{cases} d^{-\gamma} & if\ s \leq d < d_U \\ 0 & otherwise \end{cases}$$

Where γ is the Lévy shape parameter, the step length $s = 1$ the lower bound, and d_U the upper bound. In our $1000\ m^2$ landscape, $d_U = 20\sqrt{5}\ m$, the length of the diagonal of the square world.

Agents have a step length s of 1 unit distance, moving 1 unit of distance per timestep (Table 2) They stick to their sampled heading h for a number of timesteps equal to the sampled distance d.

For the first B timesteps, agents perform a close search by using a Lévy shape parameter $y_c = 3$, following a movement pattern closer to Brownian motion (James et al., 2011, Table 2). After that, agents change their Lévy shape parameter to $y_f = 2$, causing them to stick to the same heading for longer periods of time (Figure 2)

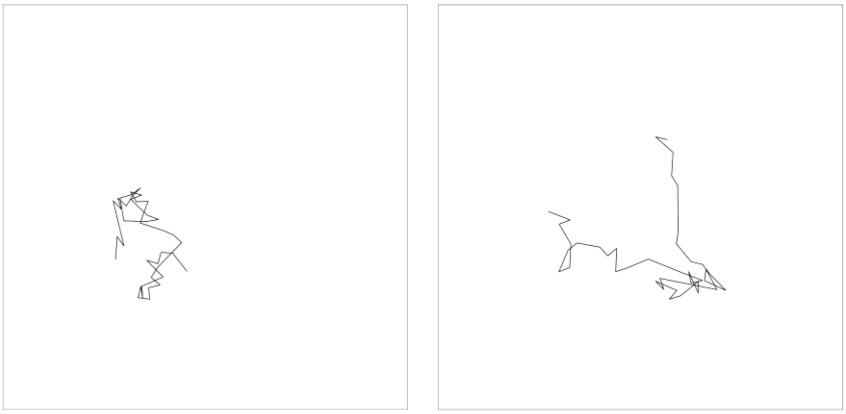

Figure 2. Examples of Lévy walks with $\gamma = 3$ (left) and $\gamma = 2$ (right) in a $1000\ m^2$ square landscape, with 40 steps of $1\ m$ step length.

During exploration, agents do not lose energy. This prevents them from dying due to exploration, rather than due to the consequences of cooperator and defector assortment across the resources. Nevertheless, the resource distribution still affects assortment through the distance and time it takes agents to travel from one resource to the next. See *Chapter 2: Assumptions underlying the model design*

Chapter 2: Assumptions underlying the model design and section *3.4.2.4 Exploration costing time but not energy* for further discussion on this.

3.1.2.4 Agent behaviour flowchart

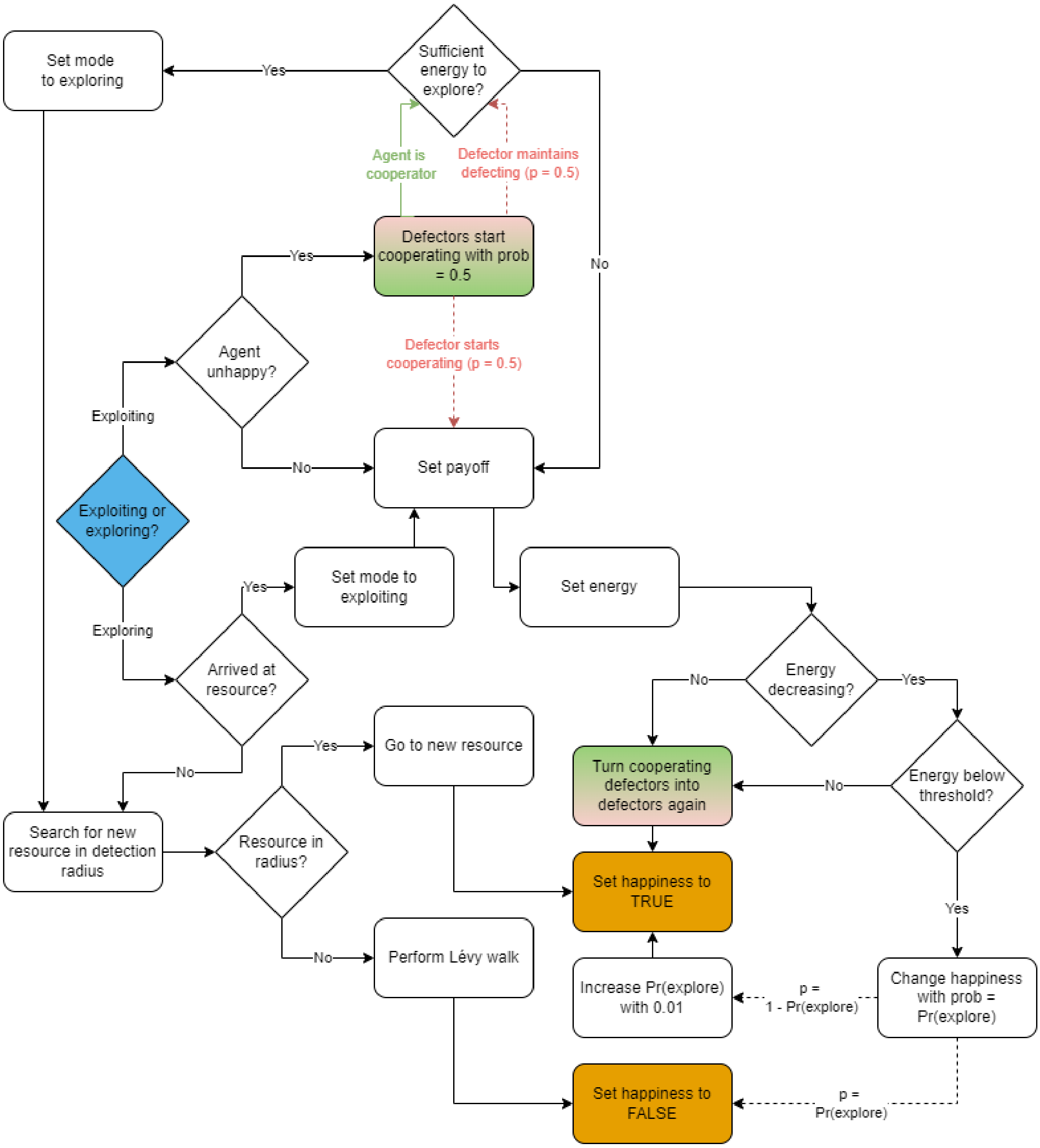

Figure 3. A flowchart of agent behaviour per timestep, starting at the blue diamond and ending at either orange rectangle. Diamonds are condition checks, rectangles are agent actions. Dashed lines indicate actions taken with a certain probability. For specifics on certain actions, refer to sections 3.1.2.2 Exploitation and 3.1.2.3 Exploration.

3.2 Simulations

3.2.1 Model initialization

At model initialization, $M = 20$ resources are placed in the world as explained in section *3.1.1.2 Resource* distributions, with resource parameters as described in Table 1 and section *3.1.1.3 Resource* qualities. Then, using a random seed, $Cnum_{tot}(0) = k * N = 160$ cooperators and $Dnum_{tot}(0) = N - (k * N) = 40$ defectors are placed on these resource, with agent parameters as described in section *3.1.2 Agent* properties.

Each model run always uses the same random seed for this initial agent placement, to make sure the influence of the *agent* distribution on assortment is kept constant. The influence of initial agent placement is minimized by the choice of a random seed with close-to-uniform agent distribution across resources, and places at least one cooperator and one defector on each resource. Note that a fully uniform agent distribution would cause all cooperators to lose and all defectors to gain the same amount of energy, causing almost all cooperators to simultaneously leave their resource at the start of the model run (see section *3.1.2.2 Exploitation*). This would result in a significant loss in energy for cooperators, and then lead to a redistribution of agents anyway.

The stochasticity present in the agents such as their random Lévy walk, decision to explore, and defectors' decision to cooperate instead of explore, are modelled using a different random seed, which changes each model run.

3.2.2 Run length

The model is ran for 2501 timesteps, from $t = 0$ to $t = 2500$. At this point, the proportion of exploring agents starts levelling off (Figure 4). This implies a settling of the assortment dynamics and should allow for enough time to adequately compare assortment across model runs.

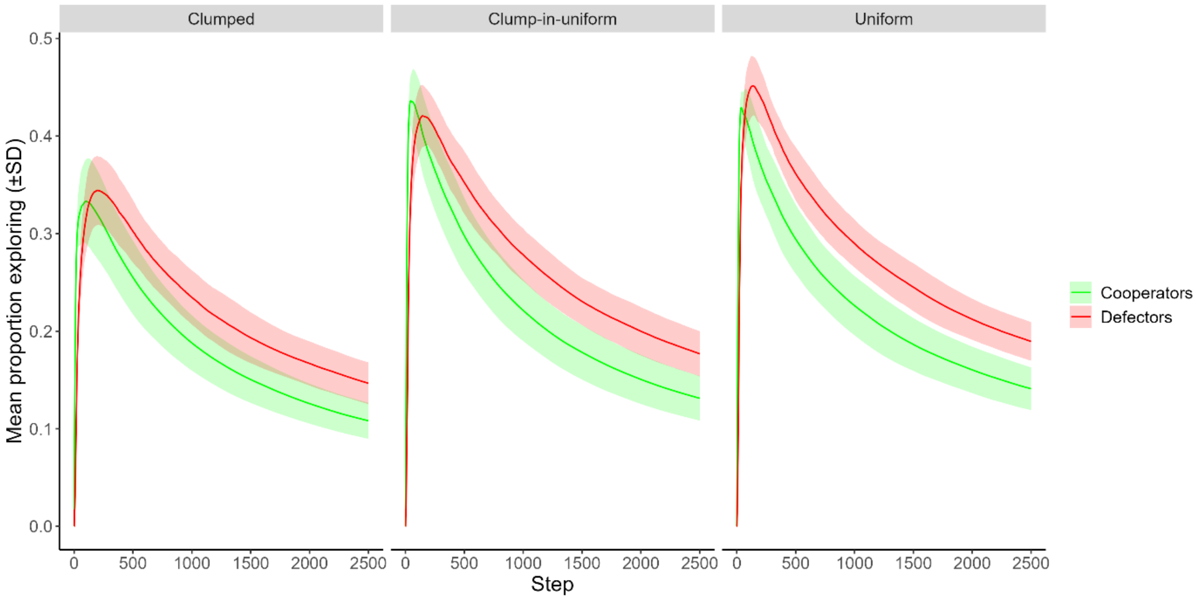

Figure 4. Timeseries of the mean proportion of agents (cooperators and defectors) that are exploring (±SD) over 100 iterations per resource distribution.

3.2.3 Iterations

Each set of parameters (as specified in section

3.5 Hypotheses) is ran for 100 iterations.

3.3 Analysis of model qualities

3.3.1 Assortment, clustering, and polarization

3.3.1.1 Assortment

Let:

- R be a set of resources
- $Cnum(r,t)$ and $Dnum(r,t)$ be the number of exploiting cooperators and defectors at resource r at timestep t, respectively
- $Cprop(r,t) := \frac{Cnum(r,t)}{Cnum(r,t)+Dnum(r,t)}$ be the cooperator proportion at resource r and timestep t
- b be the *benefit* of exploiting agents for all $r \in R$ and $t \in T$
- c be the *cost* of exploiting cooperators for all $r \in R$ and $t \in T$

We define cooperator and defector *assortment* per set of resources R and timestep t as:

$$Cassort(t,R) := \frac{\sum_{r \in R}[Cnum(r,t) * Cprop(r,t)]}{\sum_{r \in R} Cnum(r,t)} \qquad \text{(Eq 1)}$$

$$Dassort(t,R) := \frac{\sum_{r \in R}[Dnum(r,t) * Cprop(r,t)]}{\sum_{r \in R} Dnum(r,t)} \qquad \text{(Eq 2)}$$

Because cooperator payoff $Cpayoff(r,t) = Cprop(r,t) * b - c$, we can rewrite the average cooperator payoff per set of resources R and timestep t in terms of assortment ***(lemma P1)***:

$$Cpayoff_{avg}(t,R) := \frac{\sum_{r \in R}[Cnum(r,t) * Cpayoff(r,t)]}{\sum_{r \in R} Cnum(r,t)}$$

$$= \frac{\sum_{r \in R}[Cnum(r,t) * Cprop(r,t)]}{\sum_{r \in R} Cnum(r,t)} * b - c$$

$$= Cassort(t,R) * b - c$$

And similarly, because defector payoff $Cpayoff(r,t) = Cprop(r,t) * b - c$, the average defector payoff is ***(lemma P2)***:

$$Dpayoff_{avg}(t,R) := Dassort(t,R) * b$$

Positive assortment is relevant for the prisoner's dilemma because it increases average cooperator payoff (Fletcher & Doebeli, 2008). Cooperator payoff is at its lowest at a uniform agent distribution: one where each resource has the same number of cooperators and defectors. This is the lowest possible level of assortment. At a high enough level of positive assortment, $Cpayoff_{avg}(t,R) > Dpayoff_{avg}(t,R)$. However, in this thesis we are merely interested in whether positive assortment as a *potential of cooperators to compete with defectors* increases when we change the resource distribution. We can therefore loosen the constraint that average cooperator payoff must be higher than average defector payoff, and simply look at positive assortment on its own:

1. We assume the benefit b and cost c to remain constant over time and resources
2. From (1) and lemma P1 and P2, it follows that cooperator and defector payoff is determined by their assortment. ***(corollary P)***.

3.3.1.2 Assortment bounds

For each resource $r \in R$ the number of cooperators and defectors, and cooperator proportion at uniform agent distribution are:

$$Cnum_{unif}(t,R) := \frac{\sum_{r\in R} Cnum(r,t)}{|R|} \qquad \text{(Eq 3)}$$

$$Dnum_{unif}(t,R) := \frac{\sum_{r\in R} Dnum(r,t)}{|R|} \qquad \text{(Eq 4)}$$

$$Cprop_{unif}(t,R) := \frac{\sum_{r\in R} Cnum(r,t)}{\sum_{r\in R} Cnum(r,t)+\sum_{r\in R} Dnum(r,t)} \qquad \text{(Eq 5)}$$

where $|R|$ denotes the cardinality of set R.

The minimum cooperator assortment is the assortment at uniform agent distribution, expressed in terms of equations 3-5 as:

$$Cassort_{min}(t,R) := \frac{|R| * Cnum_{unif}(t,R) * Cprop_{unif}(t,R)}{|R| * Cnum_{unif}(t,R)}$$

$$= Cprop_{unif}(t,R) \qquad \text{(Eq 6)}$$

The minimum defector assortment is the assortment when $Cprop(r,t) = 0$ for all defectors and $Cprop(r,t) = 1$ for all cooperators. In other words, if $\sum_{r\in R} Cnum(r,t) \neq 0$, then $\sum_{r\in R} Dnum(r,t) = 0$. Let $R_D(t) \subseteq R$ be the set of resources on which $\sum_{r\in R_D} Dnum(r,t) \neq 0$ at timestep t. Then

$$Dassort_{min}(t,R) := \frac{\sum_{r\in R_D}[Dnum(r,t) * Cprop(r,t)] + \sum_{r\notin R_D}[Dnum(r,t) * Cprop(r,t)]}{\sum_{r\in R} Dnum(r,t)}$$

$$= \frac{0 * \sum_{r\in R_D} Dnum(r,t) + 0 * \sum_{r\notin R_D} Cprop(r,t)}{\sum_{r\in R} Dnum(r,t)} = 0 \qquad \text{(Eq 7)}$$

The maximum cooperator assortment is the same as the minimum defector assortment. Let $R_C(t) \subseteq R$ be the set of resources on which $\sum_{r\in R_C} Cnum(r,t) \neq 0$ at timestep t.Then

$$Cassort_{max} := \frac{\sum_{r\in R_C}[Cnum(r,t) * Cprop(r,t)] + \sum_{r\notin R_C}[Cnum(r,t) * Cprop(r,t)]}{\sum_{r\in R} Cnum(r,t)}$$

$$= \frac{1 * \sum_{r\in R_C} Cnum(r,t) + 0}{\sum_{r\in R} Cnum(r,t)} = 1 \qquad \text{(Eq 8)}$$

Finally, the maximum defector assortment is the same as the minimum cooperator assortment

$$Dassort_{max}(t,R) := Cprop_{unif}(t,R) \qquad \text{(Eq 9)}$$

From Equations 6-9 we conclude that $Cassort(t,R)$ (Eq 1) and $Dassort(t,R)$ (Eq 2) are bounded as follows: ***(corollary B)***:

$$0 \leq Dassort(t,R) \leq Cprop_{unif}(t,R) \leq Cassort(t,R) \leq 1$$

3.3.1.3 $Cassort(t,R)$ *as the potential of cooperators to compete with defectors*

Following corollary P, which shows that cooperator and defector payoff is determined by their assortment, we define the *potential of cooperators to compete with defectors* as $Cassort(t,R)$ (Eq 1). Note that equations 7 and 8 show that given a constant proportion of exploiting agents, i.e. given a constant $Cprop_{unif}(t,R)$, the higher $Cassort(t,R)$ is, the lower $Dassort(t,R)$. Figure 5 below shows the same.

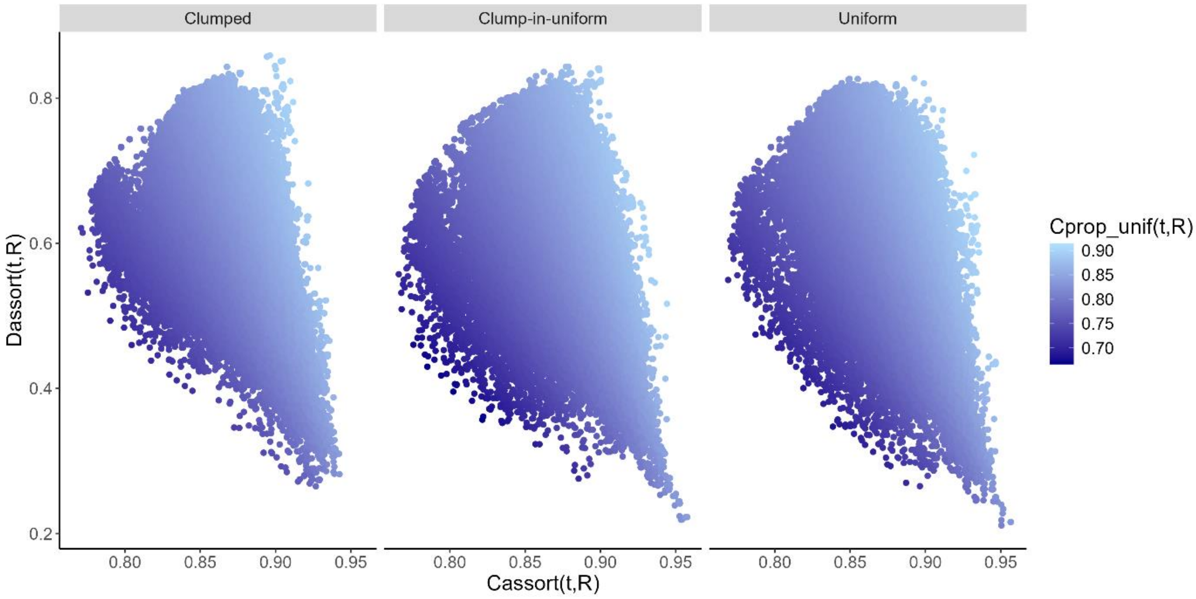

Figure 5. $Cassort(t,R)$ plotted against $Dassort(t,R)$, for 3 resource distributions, 100 iterations per distribution, and 2501 timesteps per iteration, coloured by different values of $Cprop_{unif}(t,R)$.

If we can assume $Cprop_{unif}(t,R)$ to remain relatively equal across iterations and timesteps t, we can use cooperator assortment as a variable to compare between resource distributions. Figure 6 below shows how well this assumption holds for all three resource distributions.

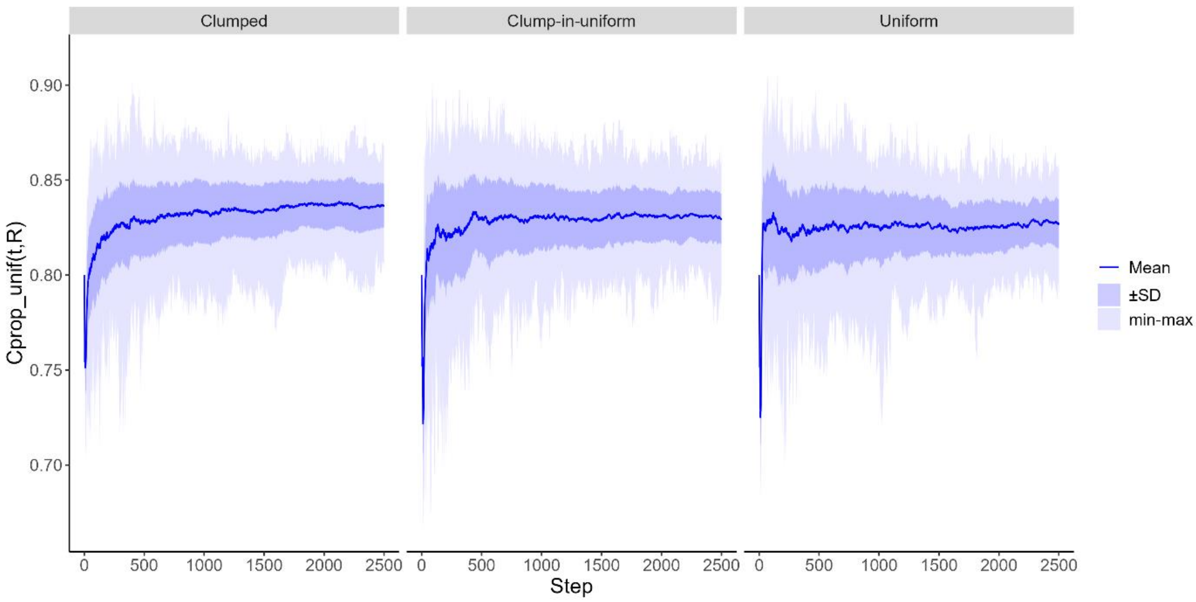

Figure 6. The mean (with ±SD and min-max range) of $Cprop_{unif}(t,R)$, for 3 resource distributions and 100 iterations per distribution.

3.3.1.4 Clustering and polarization

For assortment to take place, cooperators not only need to cluster at resources, they also need to cluster away from defectors. Indeed, from $Cassort(t, R)$ (Eq 1) and $Dassort(t, R)$ (Eq 2), it follows that assortment is determined by the number of cooperators and defectors on each resource r – $Cnum(r, t)$ and $Dnum(r, t)$, respectively – as well as the cooperator proportion $Cprop(r, t)$. We capture the first element in cooperator and defector *clustering*, and the second in *polarization*.

We define *clustering* as the higher presence of cooperators (or defectors) at some resources than at others, relative to a uniform agent distribution across a set of resources R. Using equations 3-4, we define cooperator and defector clustering at resource r and timestep t as:

$$Ccluster(r, t, R) := Cnum(r, t) - Cnum_{unif}(t, R) \quad \text{(Eq 10)}$$

$$Dcluster(r, t, R) := Dnum(r, t) - Dnum_{unif}(t, R) \quad \text{(Eq 11)}$$

We define *polarization* as a higher cooperator proportion at some resources than at others, relative to a uniform agent distribution across a set of resources R. Using equation 5, we define polarization at resource r and timestep t as:

$$Polar(r, t, R) := Cprop(r, t) - Cprop_{unif}(t, R) \quad \text{(Eq 12)}$$

Rewriting $Cassort(t, R)$ (Eq 1) and $Dassort(t, R)$ (Eq 2) in terms of equations 10-12, we get:

$$Cassort(t, R) = \frac{\sum_{r\in R}[(Ccluster(r,t,R) + Cnum_{unif}(t,R)) * (Polar(r,t,R) + Cprop_{unif}(t,R))]}{\sum_{r\in R} Cnum(r,t)} \quad \text{(Eq 13)}$$

$$Dassort(t, R) = \frac{\sum_{r\in R}[(Dcluster(r,t,R) + Dnum_{unif}(t,R)) * (Polar(r,t,R) + Cprop_{unif}(t,R))]}{\sum_{r\in R} Dnum(r,t)} \quad \text{(Eq 14)}$$

From equations 13-14, it follows that assortment can be separated into two elements, clustering and polarization ***(corollary A)***.

We use this corollary to better understand the effect of the emergent property *hoarding* on assortment. In the next section, we show that by definition, resources that we characterize as *hoarding episodes* at certain timesteps, are a potential cause of assortment in the model.

3.3.2 Hoarding

Let $Dleave(r, t)$ be the number of *departing* defectors at resource r at timestep t. Then, using equations 3-4, we define a Boolean *hoarding* at resource r and timestep t for a set of resources R as:

$$IFhoarding(r, t, R) := \quad \text{(Eq 15)}$$

$$\begin{cases} 1 \; if \; \left[\left(Cnum(r,t) + Dnum(r,t)\right) \geq \left(Cnum_{unif}(t,R) + Dnum_{unif}(t,R)\right) * 1.5\right] \wedge [Dleave(r,t) \; = 0)] \\ 0 \; otherwise \end{cases}$$

We can use equation 15 to define *hoarding* and *non-hoarding episodes*, i.e. given some set of resources R, the resources at which hoarding or non-hoarding happens:

$$HoardingEpisodes(t, R) := \sum_{r\in R} IFhoarding(r, t, R) \quad \text{(Eq 16)}$$

$$NonHoardingEpisodes(t, R) := \sum_{r\in R} (1 - IFhoarding(r, t, R)) \quad \text{(Eq 17)}$$

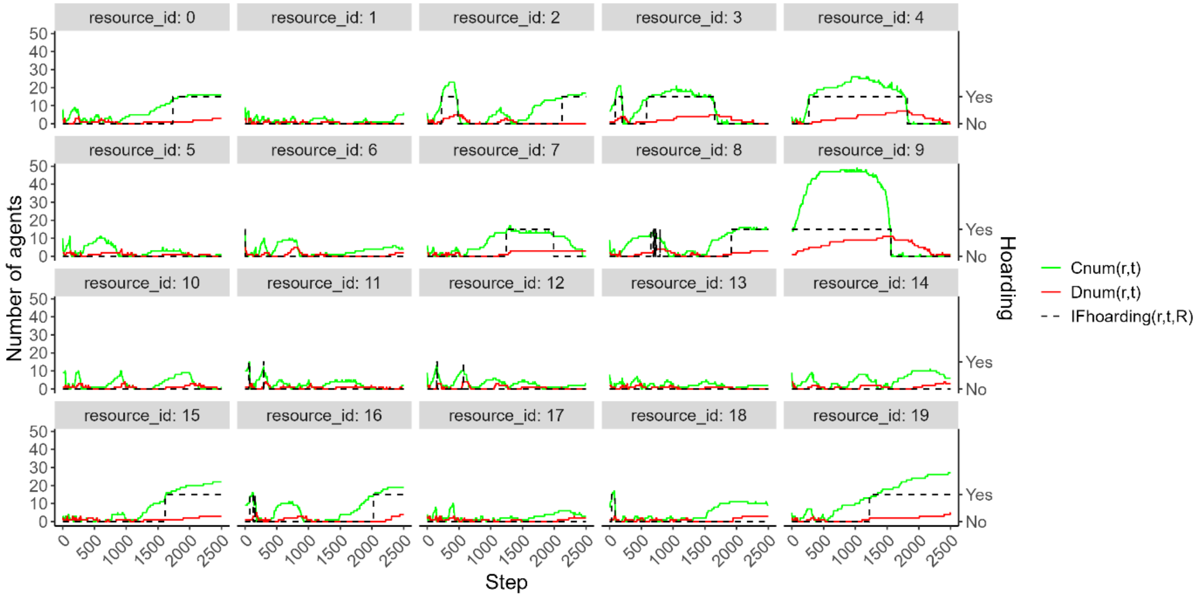

Figure 7. Hoarding episodes ($IFhoarding(r,t,R)$), number of cooperators ($Cnum(r,t)$) and number of defectors ($Dnum(r,t)$) for 20 resources $r \in R$ and 2500 timesteps

In Figure 7, we see in the plot of resource 4 that there is a hoarding episode starting after $t = 500$ and ending around $t = 2000$: the number of agents $Cnum(r,t) + Dnum(r,t)$ is relatively high, and no defectors are leaving the resource for that period. By the definitions of equations 10, 11 and 15, *clustering* is high during this hoarding episode.

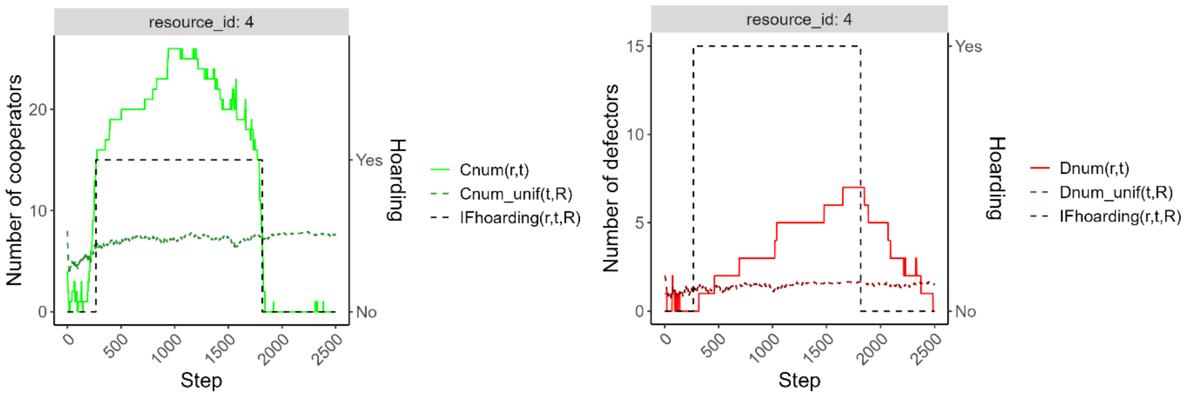

Figure 8. Hoarding episode of resource 4 from Figure 7: $IFhoarding(r,t,R)$ compared to $Cnum(r,t)$ and $Cnum_{unif}(t,R)$ (left), as well as $Dnum(r,t)$ and $Dnum_{unif}(t,R)$ (right)

Figure 8 zooms in on resource 4 and shows that $Cnum(r,t)$ and $Dnum(r,t)$ are indeed high relative to $Cnum_{unif}(t,R)$ (Eq 3) and $Dnum_{unif}(t,R)$ (Eq 4), respectively, from which follows that $Ccluster(r,t,R) > 0$ (Eq 10) and $Dcluster(r,t,R) > 0$ (Eq 11).

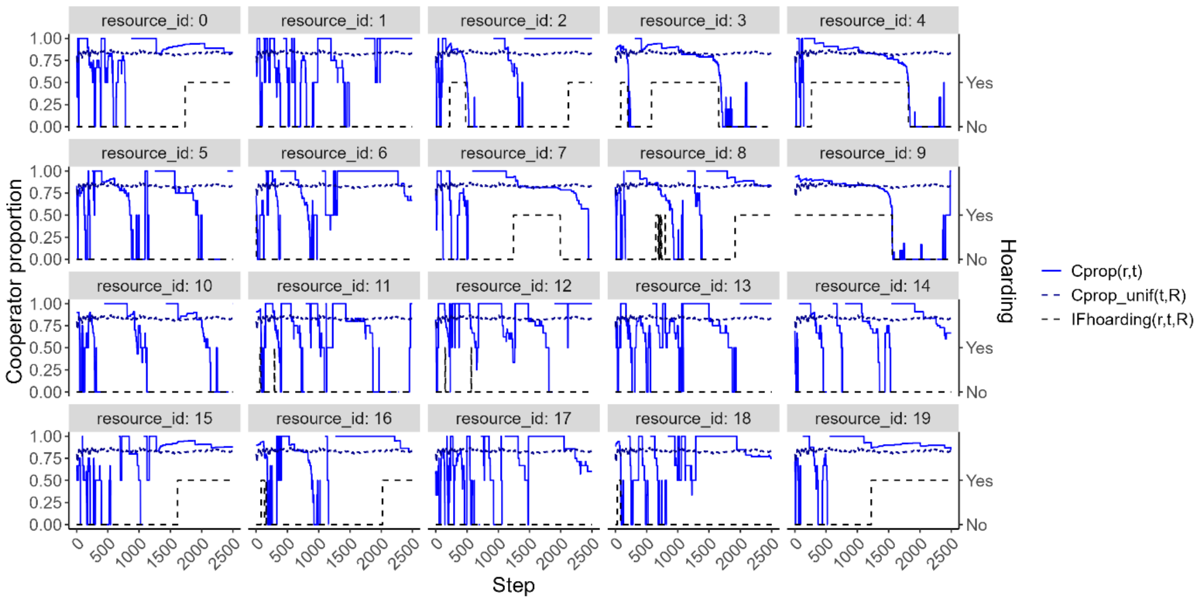

Figure 9. Hoarding episodes ($IFhoarding(r,t,R)$), cooperator proportion ($Cprop(r,t)$) and expected cooperator proportion at a uniform agent distribution ($Cprop_{unif}(t)$) for 20 resources $r \in R$ and 2500 timesteps

Figure 9 shows the same model run as Figure 7 but now compares the hoarding to $Cprop(r,t)$ and $Cprop_{unif}(t,R)$ (Eq 5). During the hoarding episode on resource 4, $Cprop(r,t)$ remains relatively constant, and mostly higher than $Cprop_{unif}(t,R)$, except for at the end. In other words, on average, $Polar(r,t) > 0$ (Eq 12). This is a consequence of the way a hoarding episode ends:

1. $Cprop(r,t)$ decreases due to incidental defector arrivals
2. As a consequence $Cpayoff(r,t)$ decreases too
3. When $Cpayoff(r,t)$ decreases below the energy threshold E_{thresh}, cooperators start leaving
4. As a consequence $Cprop(r,t)$ decreases further, and $Dpayoff(r,t)$ with it
5. When $Dpayoff(r,t)$ decreases below the energy threshold E_{thresh}, defectors start leaving

Step 5 violates the second condition of equation 15, $Dleave(r,t) = 0$, and ends the hoarding episode.

From the definitions of hoarding and assortment, it follows that the two are interrelated. We use the clustering and polarization measures of equations 10-12, the definitions of hoarding and hoarding episodes of equations 15-17, and corollary A, to compare assortment on hoarding episodes or non-hoarding episodes.

3.4 Sensitivity, robustness, and dispersion analysis

3.4.1 Sensitivity analysis

The default parameter values have been chosen to cause cooperator assortment. An open question is how sensitive cooperator assortment is to changes in these values. Manzo defines sensitivity analysis as “the assessment of the variability of the ABM’s simulated outcomes as a function of the model’s parameter values” (2022a). Indeed, it is entirely possible for other values or models to lead to more or less assortment. However, the primary goal of this thesis is not to *explain* cooperator assortment, but to determine – in case there *is* assortment – how large the influence of the resource distribution is. A full sensitivity analysis is not feasible within the time constraints of this project. Nevertheless, in this section we provide a rudimentary analysis that justifies the particular payoff structure we have chosen.

In section *3.1.2.2 Exploitation*, we calculated the cooperator and defector payoff at uniform agent distribution as a simplified average payoff per type:

$$Cpayoff_{avg}(t, R) \approx k * b - c = 0.8 * 2 - 0.5 = 1.1$$

$$Dpayoff_{avg}(t, R) \approx k * b = 0.8 * 2 = 1.6$$

where $k = 0.8$ is the initial cooperator proportion, $b = 2$ the benefit and $c = 0.5$ the cost of exploitation (Table 2). We define the average change in energy for cooperators and defectors as

$$\Delta E_{Cavg}(t, R) := Cpayoff_{avg}(t, R) - E_{loss}$$

$$\Delta E_{Davg}(t, R) := Dpayoff_{avg}(t, R) - E_{loss}$$

and note that for the default parameter values, $\Delta E_{Cavg}(t, R) = -0.1$ and $\Delta E_{Davg}(t, R) = 0.4$ (Table 2). Changing any parts of the above equations will change the dynamics, but we are only interested in dynamics in which, on average, defectors outcompete cooperators, and which cause assortment. If either type of agents loses or gains too much energy, no assortment will take place. More specifically, cooperators need – on average – an incentive to "move away from" defectors. By definition of being defectors, defectors have an inherent incentive to "follow" cooperators. Note that "following" and "moving away from" are not conscious efforts. Neither cooperators nor defectors have the capacity to detect other agents directly. All they detect is their payoff, and whether it is high enough for them to gain energy. The cooperators' incentive needs to therefore be given by its average energy loss.

Within these confines, different combinations of values of k, b, c, and E_{loss} are possible. We put the following constraints on these combinations:

1. Changing k will change $Cprop(r, t)$ and thus change $Cassort(t, R)$ by definition (see section *3.3.1.1 Assortment*, equation 1). We therefore keep $k = 0.8$ as fixed.
2. As per Fletcher and Doebeli, $b > c > 0$ (2008)
3. For assortment to take place, we require $\Delta E_{Cavg}(t, R) < 0$ and $\Delta E_{Davg}(t, R) > 0$
4. Let $\frac{c}{b} \geq 0.1$, so that cooperation cost is never less than 10% of exploitation benefit

We can keep the difference between $\Delta E_{Cavg}(t, R)$ and $\Delta E_{Davg}(t, R)$ constant by keeping c constant. Combined with constraint 4, this sets a range for the exploitation benefit as $0.5 < b \leq 5$. Given the other constraints, for each b, the possible values of exploitation energy loss are

$$\frac{1}{10}(8b - 5) < E_{loss} < \frac{4b}{5}$$

Note that changing c means changing b and thus changing E_{loss} along with it. This will therefore only speed up or slow down the assortment dynamics relative to the number of timesteps, rather than change the difference in payoff between cooperators and defectors. The latter is done by changing the proportion $\frac{c}{b}$, which we do by changing b relative to a fixed c.

With steps of $\Delta b = 0.5$ and $\Delta E_{loss} = 0.1$, we test the outcomes of the following combinations of b and E_{loss} as listed in Table 3.

Table 3. The values of b and E_{loss} used in the analysis of the payoff structure.

$\boldsymbol{b}$	$\boldsymbol{E_{loss}}$
1	$\{\frac{4}{10},\frac{5}{10},\frac{6}{10},\frac{7}{10}\}$
1.5	$\{\frac{8}{10},\frac{9}{10},\frac{10}{10},\frac{11}{10}\}$
2	$\{\frac{12}{10},\frac{13}{10},\frac{14}{10},\frac{15}{10}\}$
2.5	$\{\frac{16}{10},\frac{17}{10},\frac{18}{10},\frac{19}{10}\}$
3	$\{\frac{20}{10},\frac{21}{10},\frac{22}{10},\frac{23}{10}\}$
3.5	$\{\frac{24}{10},\frac{25}{10},\frac{26}{10},\frac{27}{10}\}$
4	$\{\frac{28}{10},\frac{29}{10},\frac{30}{10},\frac{31}{10}\}$
4.5	$\{\frac{32}{10},\frac{33}{10},\frac{34}{10},\frac{35}{10}\}$
5	$\{\frac{36}{10},\frac{37}{10},\frac{38}{10},\frac{39}{10}\}$

For each combination of parameters in Table 3, we calculate the mean $Cassort(t, R)$ and $HoardingEpisodes(t, R)$ per timestep, as well as the proportion of dead cooperators at the end of the model run, all averaged over 100 iterations. Otherwise, we use the default parameter values as listed in Table 1 and Table 2. In the results, for each value of b, we indicate 4 possible values of E_{loss} as “very low”, “low”, “high”, and “very high”, respectively. Parameter combinations for which in any of the iterations all defectors died before the end of the model run, are left out of the analysis.

Note that due to the ability of cooperators to exploit a resource on their own, the proportion of cooperator deaths is not as affected as the proportion of defector deaths, and did not go over 0.06 for any of the parameter combinations and iterations.

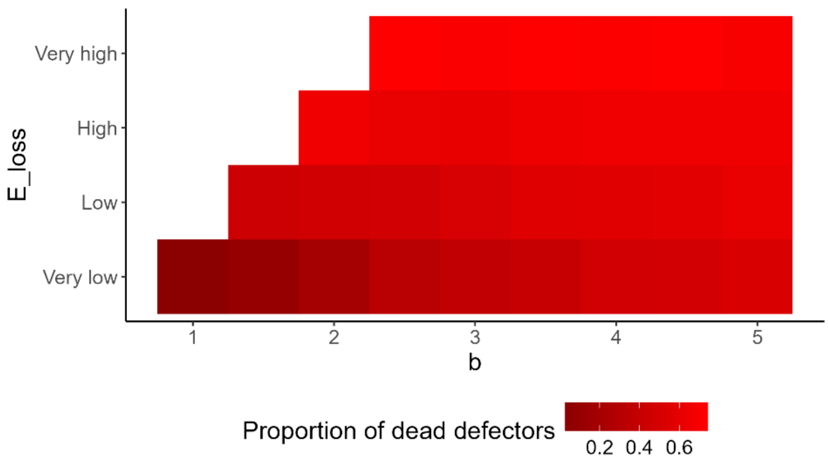

Figure 10. The proportion of dead defectors at the end of the model run, averaged over 10 iterations, for different combinations of b and E_{loss}.

The results show that a cost-to-benefit proportion of 0.25 or higher can cause the death of all defectors before the model run is over, depending on the value of E_{loss} (Figure 10). The lowest proportion of dead defectors is found when $b = 1$ and $E_{loss} = 0.4$ (very low). The default parameter values result in the third lowest proportion of defectors deaths. Note that for each value of b, the proportion of dead defectors increases when we increase E_{loss}. Given a cost of $c = 0.5$, an average change in energy of $\Delta E_{Cavg}(t, R) = -0.1$ for cooperators and $\Delta E_{Davg}(t, R) = 0.4$ for defectors therefore seems optimal to keep defector deaths low, regardless of the relative amount of benefit.

Similarly, for each value of b, the mean $Cassort(t, R)$ per timestep increases when we increase E_{loss} (Figure 11). It is lowest for the default parameter values. By definition, $Cassort(t, R)$ is affected by the proportion of cooperators (section *3.3.1.1 Assortment*). On average, this proportion will increase when the number of defector deaths increases relative to the number of cooperator deaths. The proportion of defector deaths therefore has the potential to influence $Cassort(t, R)$ through $Cprop_{unif}(t, R)$ – see section *5.1 General conclusions* for a discussion on this.

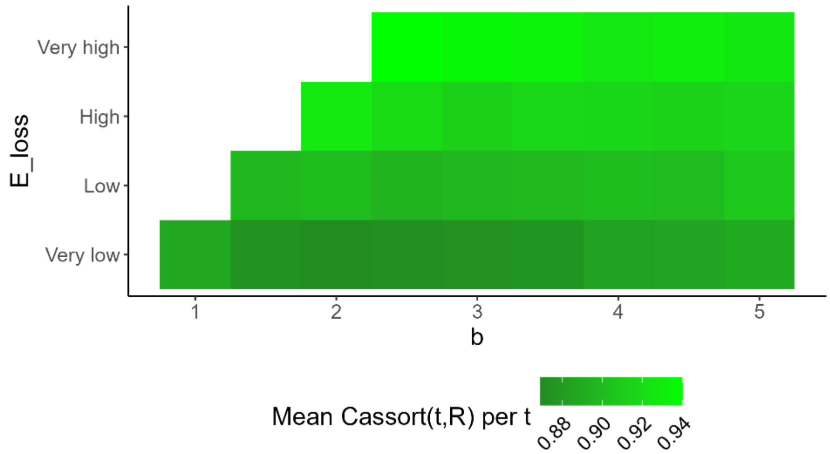

Figure 11. Mean $Cassort(t, R)$ per timestep, averaged over 10 iterations, for different combinations of b and E_{loss}.

For each value b, the mean $HoardingEpisodes(t, R)$ per timestep decreases when we increase E_{loss} (Figure 12. Mean $HoardingEpisodes(t, R)$ per timestep, averaged over 10 iterations, for different combinations of b and E_{loss}.Figure 12). The more energy loss, the less possibility agents have to hoard energy.

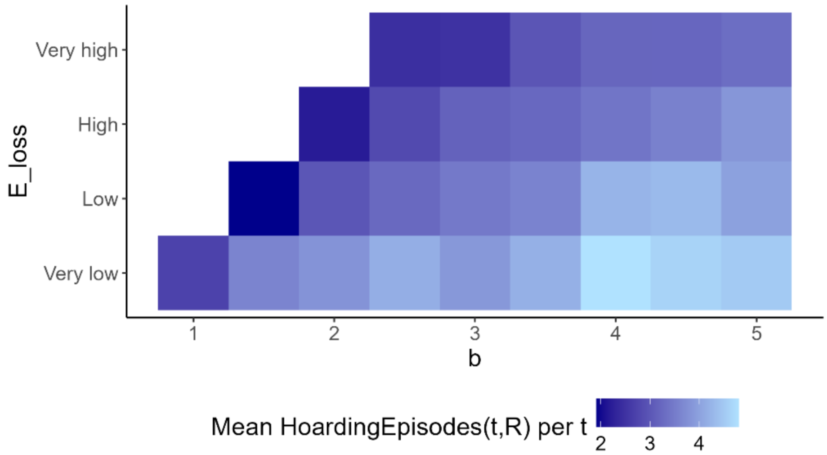

Figure 12. Mean $HoardingEpisodes(t, R)$ per timestep, averaged over 10 iterations, for different combinations of b and E_{loss}.

3.4.2 Robustness analysis

A distinction can be made between a model's parameters and its *internal details* (Manzo, 2022a). A sensitivity analysis is concerned with the former, a robustness analysis with the latter. For example, the initial amount of energy agents start out with is a parameter, while what happens to agents when their energy gets to zero or keeps increasing is an internal detail of the model. In this section, we provide an overview and justification of some of the choices made in the model design.

3.4.2.1 No energy cap

In the model, agents' energy can keep increasing indefinitely. The main reason for this is to keep the public goods game played by the exploiting agents as simple as possible, without making any additional assumptions about what it means to "cooperate" or "defect". A model with a max agent energy capacity would need to answer the question what agents do when their energy reaches this capacity. Agents can only sit idle for one timestep, when they will immediately start losing energy again. Does a fully satisfied cooperator still contribute to the payoff of other agents? Essentially, a cap on energy punishes whichever type of agent is doing best, and deamplifies assortment dynamics.

Nevertheless, it is unrealistic to assume infinite inflow of energy into a system. See section *5.2 Energy conservation* for a discussion on this.

3.4.2.2 Agent death

A similar consideration must be made for the outflow of energy: what happens when an agent's energy reaches zero? As stated in

Chapter 2: Assumptions underlying the model design, agent properties are assumed to be *minimal* and *fixed* and the model therefore cannot include any evolutionary dynamics. On the other hand, a model design in which agents cannot die raises the question what agents can and should do while their energy is zero. Like an energy cap, this would deamplify assortment dynamics.

Agent deaths, through agent removal from the model, on the other hand, are *part of* the assortment dynamics. As we have seen in section *3.3.1 Assortment, clustering, and polarization*, the (potential) proportion of cooperators to defectors directly affects the measure of assortment used. As long as agents do not die at such a rate it immediately and completely changes the initial parameter values, agent deaths are considered a logical part and consequence of the assortment dynamics. As we have seen in section *3.4.1 Sensitivity analysis*, this is indeed not the case. We refer the reader to section *5.1 General conclusions* for a further discussion on this.

3.4.2.3 Defectors' ability to cooperate

As a consequence of assortment dynamics, defectors will sometimes end up at resources without any cooperators. It is unrealistic to assume any agent not to be able to exploit a resource given no opportunity to defect: even the most selfish agent would put in the energy of exploitation if necessary. However, given the assumption of *minimal* and *fixed* agent perspectives as outlined in

Chapter 2: Assumptions underlying the model design, agent cannot observe other agents. To nevertheless still allow defectors a chance to survive presence on a resource without cooperators, they have a probability to temporarily cooperate (see section *3.1.2.2 Exploitation* for details).

3.4.2.4 Exploration costing time but not energy

The research question of this thesis requires the model to have some *spatial* element across which resources can be distributed. More specifically, it requires this spatial element to somehow affect assortment dynamics. This is the case when agents lose energy while travelling between resources: the more space there is between resources, the more energy there is to lose. However, this causes a disproportionate amount of agents to die. Although it can be argued that these deaths are a consequence of the resource distribution, they are *also* a consequence of exploration dynamics, which includes the type of random walk used. Because this thesis is not intended to research the influence of random walks on assortment dynamics, agents do not lose energy while exploring.

The spatial element of the model can also affect assortment dynamics through the *time* it takes agents to travel from one resource to another. Exploring agents are not part of the assortment measure as defined in section *3.3.1.1 Assortment*, and therefore influence assortment. The more time defectors take to explore, the more time cooperators have to assort themselves positively. As stated in

Chapter 2: Assumptions underlying the model design, these elements of *time* and *timing* are key in the model design.

3.4.3 Dispersion analysis

A dispersion analysis is meant to evaluate the variability in cooperator assortment across multiple iterations with the same parameter values (Manzo, 2022a). This is done explicitly by running the model for 100 iterations for each resource distribution, an applying an Analysis of Variance (ANOVA). We refer the reader to *Chapter 4: Results*.

3.5 Hypotheses

Let RU, RC, and RCU be the sets of resources in the uniform, clumped, and clump-in-uniform resource distributions, respectively, and T_{full} be the set of all timesteps in an iteration, from 0 to 2500.

The **main hypothesis** is that the resource distribution $R \in \{RC, RCU, RU\}$ affects the cooperator assortment $Cassort(t, R)$ (Figure 13), in such a way that assortment is highest in resource distribution RC, then in RCU, and lowest in RU:

$$\sum_{t \in T_{full}} Cassort(t, RC) > \sum_{t \in T_{full}} Cassort(t, RCU) > \sum_{t \in T_{full}} Cassort(t, RU) \qquad \text{(Theorem 1)}$$

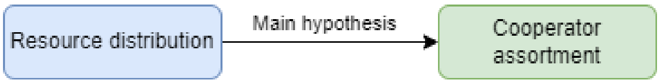

Figure 13. Diagram showing the causal link referred to in the main hypothesis.

We know that hoarding and assortment are interrelated (see section *3.3.2 Hoarding*). This raises questions on what role hoarding has to play in the result of theorem 1. Because hoarding is an emergent property and not a parameter we can control, we cannot test hypotheses pertaining to the effect of hoarding on assortment directly. We can however measure assortment on hoarding and non-hoarding episodes separately. This gives rise to two hypotheses regarding the influence of the resource distribution on hoarding and non-hoarding cooperator assortment (Figure 14).

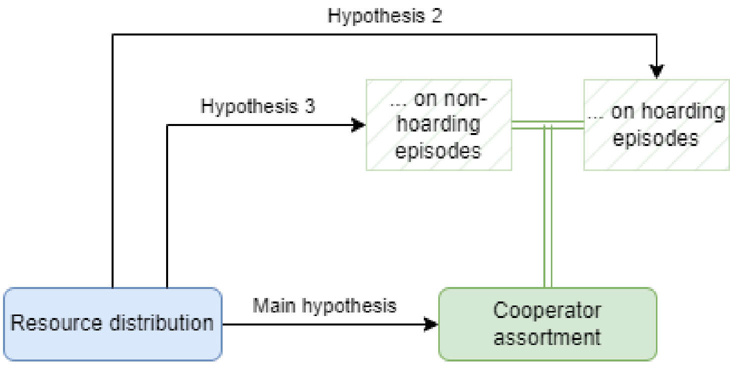

Figure 14. Diagram showing the way cooperator assortment can be divided into assortment on hoarding and on non-hoarding episodes (green boxes), as well as the causal links referred to in the main hypothesis and hypotheses 2 and 3 (solid arrows).

Note that $Cassort(t, R)$ is a model-wide measure and therefore cannot be used to measure assortment on a subset of resources in the model. Following corollary A, we make use of the clustering and polarization measures defined in equations 10-12. Specifically, we define average clustering and polarization per (non-)hoarding episode as:

$$AvgHoardingCcluster(t, R) := \frac{\sum_{r \in R}[IFhoarding(r,t,R) * abs(Ccluster(r,t,R))]}{HoardingEpisodes(t,R)} \qquad \text{(Eq 18)}$$

$$AvgHoardingPolar(t, R) := \frac{\sum_{r \in R}[IFhoarding(r,t,R) * abs(Polar(r,t,R)]}{HoardingEpisodes(t,R)} \qquad \text{(Eq 19)}$$

$$AvgNonHoardingCcluster(t, R) := \frac{\sum_{r \in R}[(1 - IFhoarding(r,t,R)) * abs(Ccluster(r,t,R))]}{NonHoardingEpisodes(t,R)} \qquad \text{(Eq 20)}$$

$$AvgNonHoardingPolar(R, T) := \frac{\sum_{r \in R}[(1 - IFhoarding(r,t,R)) * abs(Polar(r,t,R))]}{NonHoardingEpisodes(t,R)} \qquad \text{(Eq 21)}$$

Hypothesis 2 is that the resource distribution $R \in \{RC, RCU, RU\}$ *does not affect* the average clustering and polarization per hoarding episode:

$$\sum\nolimits_{t\in T_{full}} AvgHoardingCcluster(t, RC)$$
$$\approx \sum\nolimits_{t\in T_{full}} AvgHoardingCcluster(t, RCU)$$
$$\approx \sum\nolimits_{t\in T_{full}} AvgHoardingCcluster(t, RU) \qquad \text{(Theorem 2a)}$$

$$\sum\nolimits_{t\in T_{full}} AvgHoardingPolar(t, RC)$$
$$\approx \sum\nolimits_{t\in T_{full}} AvgHoardingPolar(t, RCU)$$
$$\approx \sum\nolimits_{t\in T_{full}} AvgHoardingPolar(t, RU) \qquad \text{(Theorem 2b)}$$

Hypothesis 3 is that the resource distribution $R \in \{RC, RCU, RU\}$ affects the average clustering and polarization per non-hoarding episode, in such a way that clustering and polarization are highest in resource distribution RC, then in RCU, and lowest in RU:

$$\sum\nolimits_{t\in T_{full}} AvgNonHoardingCcluster(t, RC)$$
$$> \sum\nolimits_{t\in T_{full}} AvgNonHoardingCcluster(t, RCU)$$
$$> \sum\nolimits_{t\in T_{full}} AvgNonHoardingCcluster(t, RU) \qquad \text{(Theorem 3a)}$$

$$\sum\nolimits_{t\in T_{full}} AvgNonHoardingPolar(t, RC)$$
$$> \sum\nolimits_{t\in T_{full}} AvgNonHoardingPolar(t, RCU)$$
$$> \sum\nolimits_{t\in T_{full}} AvgNonHoardingPolar(t, RU) \qquad \text{(Theorem 3b)}$$

Although we cannot test the effect of hoarding on cooperator assortment directly, we *can* measure the correlation between the two, which we call the **quality** of hoarding. We can then test the effect of the resource distribution on both the *quantity* and the *quality* of hoarding, which gives rise to the final two hypotheses (Figure 15).

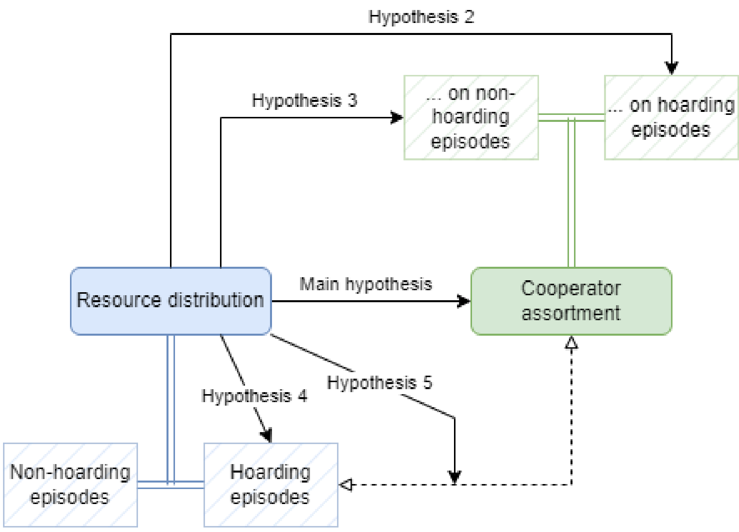

Figure 15. Diagram showing the way cooperator assortment can be divided into assortment on hoarding and on non-hoarding episodes (green boxes), the way resources are made up of hoarding and non-hoarding episodes (blue boxes), the correlation between the amount of hoarding and cooperator assortment (dashed arrow) as well as all the causal links referred to in the five hypotheses (solid arrows).

Let $Cenergy(r, t)$ and $Denergy(r, t)$ be the amount of cooperator and defector energy, respectively, at resource r at timestep t. Then for any set of resources R and timesteps T, we define the average number of hoarding agents and hoarding energy per hoarding episode as follows:

$$AvgHoardingAgents(t, R) := \frac{\sum_{r \in R}[IFhoarding(r,t,R) * (Cnum(r,t) + Dnum(r,t))]}{HoardingEpisodes(t,R)} \quad \text{(Eq 22)}$$

$$AvgHoardingEnergy(t, R) := \frac{\sum_{r \in R}[IFhoarding(r,t,R) * (Cenergy(r,t) + Denergy(r,t))]}{HoardingEpisodes(t,R)} \quad \text{(Eq 23)}$$

We define hoarding quantity and quality as follows:

- Hoarding *quantity* is the number of hoarding episodes, and average hoarding agents and hoarding energy per hoarding episode (equations 16, 22, and 23)
- Hoarding *quality* is the Pearson correlation coefficient ρ between number of hoarding agents and assortment, defined for a resource distribution R as:

$$\rho_{X(R),Y(R)} = \frac{cov(X(R), Y(R))}{\sigma_{X(R)}\sigma_{Y(R)}} \quad \text{(Eq 24)}$$

with $X(R) = \sum_{t \in T_{full}} \sum_{r \in R}[IFhoarding(r, t, R) * (Cnum(r, t) + Dnum(r, t))]$

and $Y(R) = \sum_{t \in T_{full}} Cassort(t, R)$

Hypothesis 4 is that the resource distribution $R \in \{RC, RCU, RU\}$ *does not affect* the hoarding *quantity*:

$$\sum_{t \in T_{full}} HoardingEpisodes(t, RC)$$
$$\approx \sum_{t \in T_{full}} HoardingEpisodes(t, RCU)$$
$$\approx \sum_{t \in T_{full}} HoardingEpisodes(t, RU) \quad \text{(Theorem 4a)}$$

$$\sum_{t \in T_{full}} AvgHoardingAgents\ (RC)$$
$$\approx \sum_{t \in T_{full}} AvgHoardingAgents(t, RCU)$$
$$\approx \sum_{t \in T_{full}} AvgHoardingAgents(t, RU) \quad \text{(Theorem 4b)}$$

$$\sum_{t \in T_{full}} AvgHoardingEnergy(t, RC)$$
$$\approx \sum_{t \in T_{full}} AvgHoardingEnergy(t, RCU)$$
$$\approx \sum_{t \in T_{full}} AvgHoardingEnergy(t, RU) \quad \text{(Theorem 4c)}$$

Hypothesis 5 is that the resource distribution $R \in \{RC, RCU, RU\}$ affects the hoarding *quality*, in such a way that the Pearson correlation coefficient between hoarding and cooperator assortment is highest in resource distribution RC, then in RCU, and lowest in RU:

$$\rho_{X(RC),Y(RC)} > \rho_{X(RCU),Y(RCU)} > \rho_{X(RU),Y(RU)} \quad \text{(Theorem 5)}$$

with $X(R) = \sum_{t \in T_{full}} \sum_{r \in R}[IFhoarding(r, t, R) * (Cnum(r, t) + Dnum(r, t))]$

and $Y(R) = \sum_{t \in T_{full}} Cassort(t, R)$

From theorem 1, it follows that assortment is higher in more clumped resource distributions. From theorem 2 and 3, and corollary A, it follows that this increase in assortment is due to an increase in assortment on non-hoarding episodes. From theorem 4a-c, it follows that the higher assortment in clumped resource distributions as shown in theorems 1-3 is *not* due to a difference in hoarding *quantity*. From theorem 5, we can conclude that the higher assortment in clumped resource distributions is accompanied by a higher hoarding *quality*.

Chapter 4: Results

For the analyses, we first use a one-way ANOVA and then a post-hoc pairwise (two-tailed) t-test with Bonferroni correction to control for the type I error rate. For this, we use the 'aov' function from the built-in R package *stats*, and the 'pairwise_t_test' function from the R package *rstatix* with 'p.adjust.method = "bonferroni"' and 'paired = FALSE' (Kassambara, 2021; R Core Team, 2022). We report the p-value as well as the effect size using Cohen's d, by applying the 'cohens_d' function from the R package *rstatix* with 'var.equal = TRUE' (Cohen, 1988; Kassambara, 2021).

Because our data are simulated, we assume the data to be independent. Furthermore, we check that...

- ... the residuals are normally distributed, by inspecting a density and Q-Q plot, and doing a Shapiro-Wilk test
- ... the three resource distributions have equal variance, by doing a Levene's test

Q-Q plots are created using the 'ggqqplot' function from the R package *ggpubr* (Kassambara, 2020). Shapiro-Wilk and Levene's tests are applied using the functions 'shapiro_test' and 'levene_test' from the R package *rstatix* (Kassambara, 2021)

When suitable, we transform the data to a normal distribution. Any other deviations from the above assumptions are reported as well. With the large sample size used in our analyses, ANOVA and t-test can deal with small deviations from these assumptions (Blanca et al., 2017, 2018).

4.1 Main hypothesis

The initial ANOVA indicates a significant difference in $Cassort(t, R)$ between resource distributions ($F(2, 297) = 12.87$, $p < 0.001$). A pairwise t-test shows a significant difference between clumped and uniform resource distributions (adjusted $p < 0.001$) with moderate effect size (Cohen's $d = 0.737$) (Figure 16).

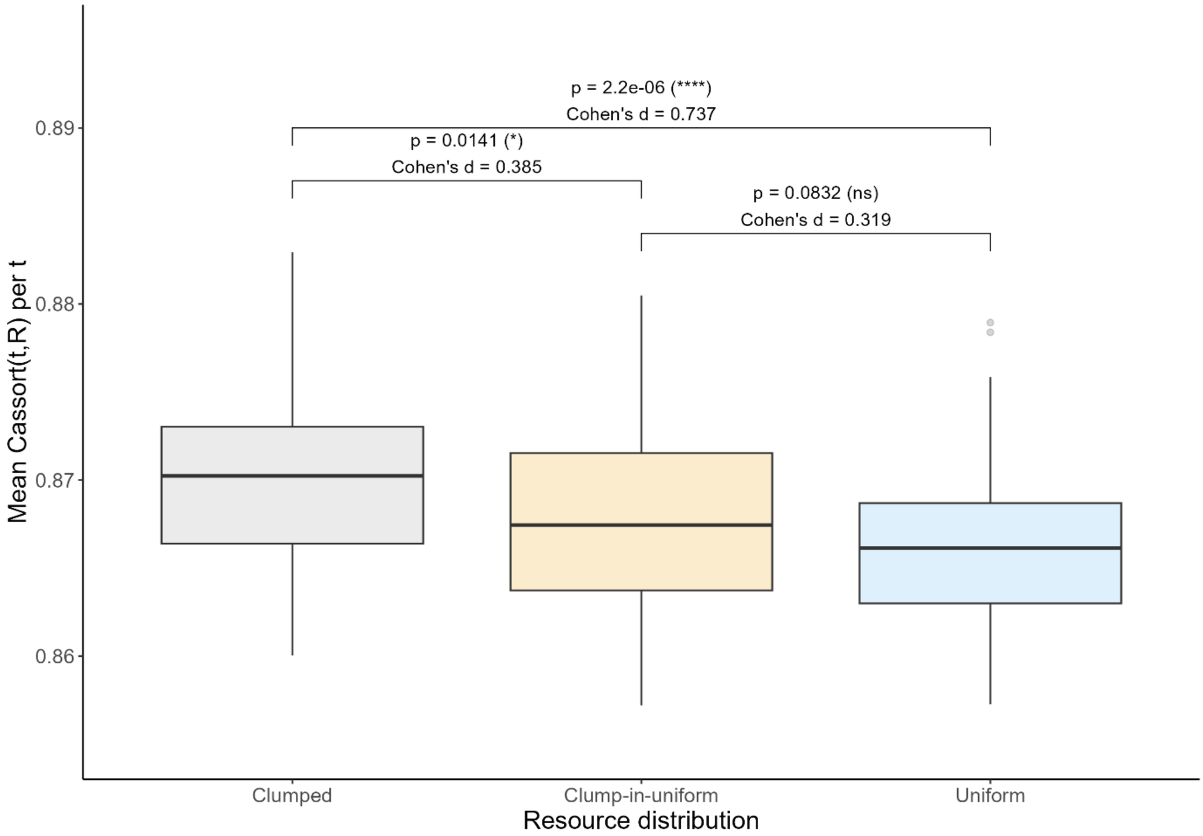

Figure 16. Boxplots of the mean $Cassort(t, R)$ per timestep, for three resource distributions and 100 iterations per distribution, along with the results (adjusted p-value with Bonferroni correction and Cohen's d) of the pairwise t-tests.

A significant difference was also found between clumped and clump-in-uniform resource distributions (adjusted p = 0.014), but effect size was small (Cohen's d = 0.385). Difference between clump-in-uniform and uniform resource distributions was non-significant (adjusted p = 0.083).

A Shapiro-Wilk test indicates a small deviation from normality (W = 0.989, p = 0.018), but visual inspection of the density and Q-Q plot of the residuals shows a close to normal distribution. A Levene's test indicates equal variance between distributions (F = 2.25, p = 0.107).

4.2 Hypothesis 2

4.2.1 Theorem 2a

After applying a reciprocal transformation ($\frac{1}{x}$), the initial ANOVA indicates no difference in $AvgHoardingCcluster(t, R)$ between resource distributions (F(2, 297) = 0.96, p = 0.384). A pairwise t-test confirms this, showing no significant differences between any of the resource distributions (Figure 17).

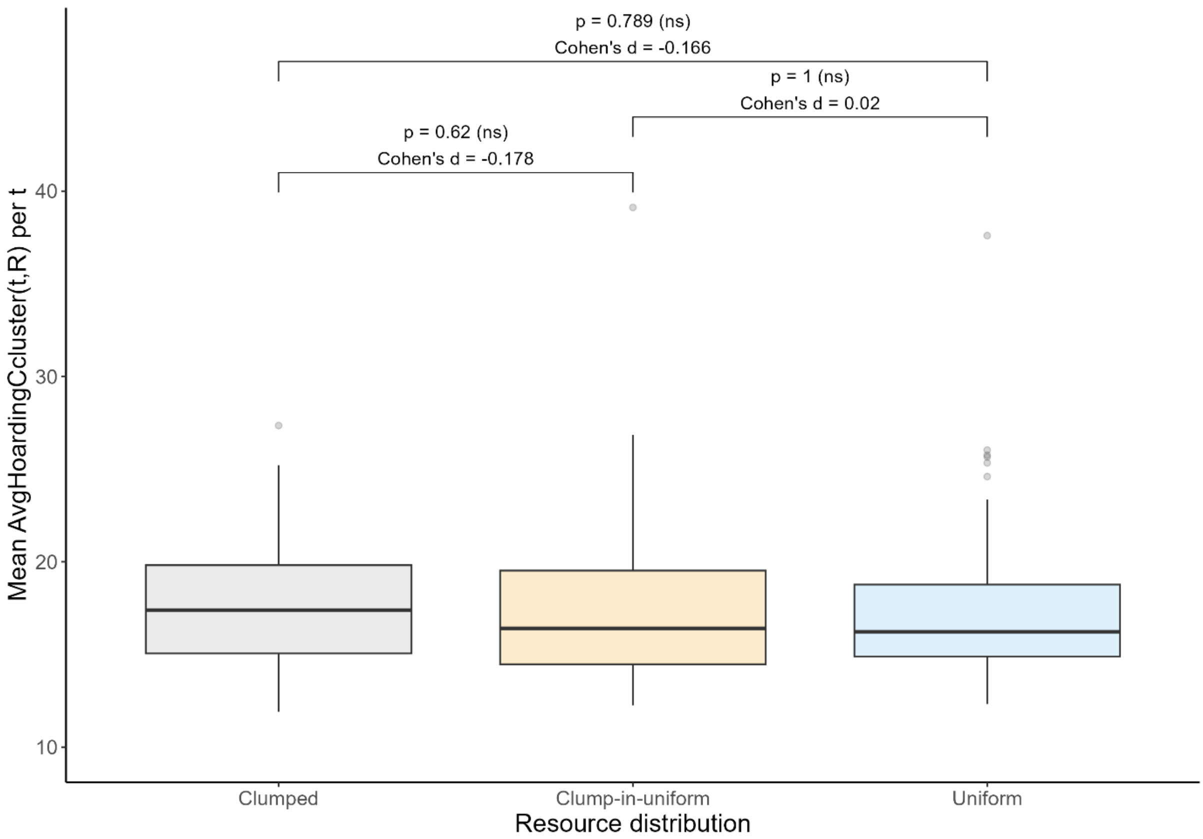

Figure 17. Boxplots of the mean $AvgHoardingCcluster(t, R)$ per timestep, for three resource distributions and 100 iterations per distribution, along with the results (adjusted p-value with Bonferroni correction and Cohen's d) of the pairwise t-tests.

A Shapiro-Wilk test indicates a small deviation from normality (W = 0.989, p = 0.020), but visual inspection of the density and Q-Q plot of the residuals shows a close to normal distribution. A Levene's test indicates equal variance between distributions (F = 0.842, p = 0.432).

4.2.2 Theorem 2b

The initial ANOVA indicates a significant difference in $AvgHoardingPolar(t, R)$ between resource distributions (F(2, 297) = 5.156, p = 0.006). A pairwise t-test shows a significant difference between clumped and uniform resource distributions (adjusted p = 0.005) with small effect size (Cohen's d = -0.458) (Figure 18).

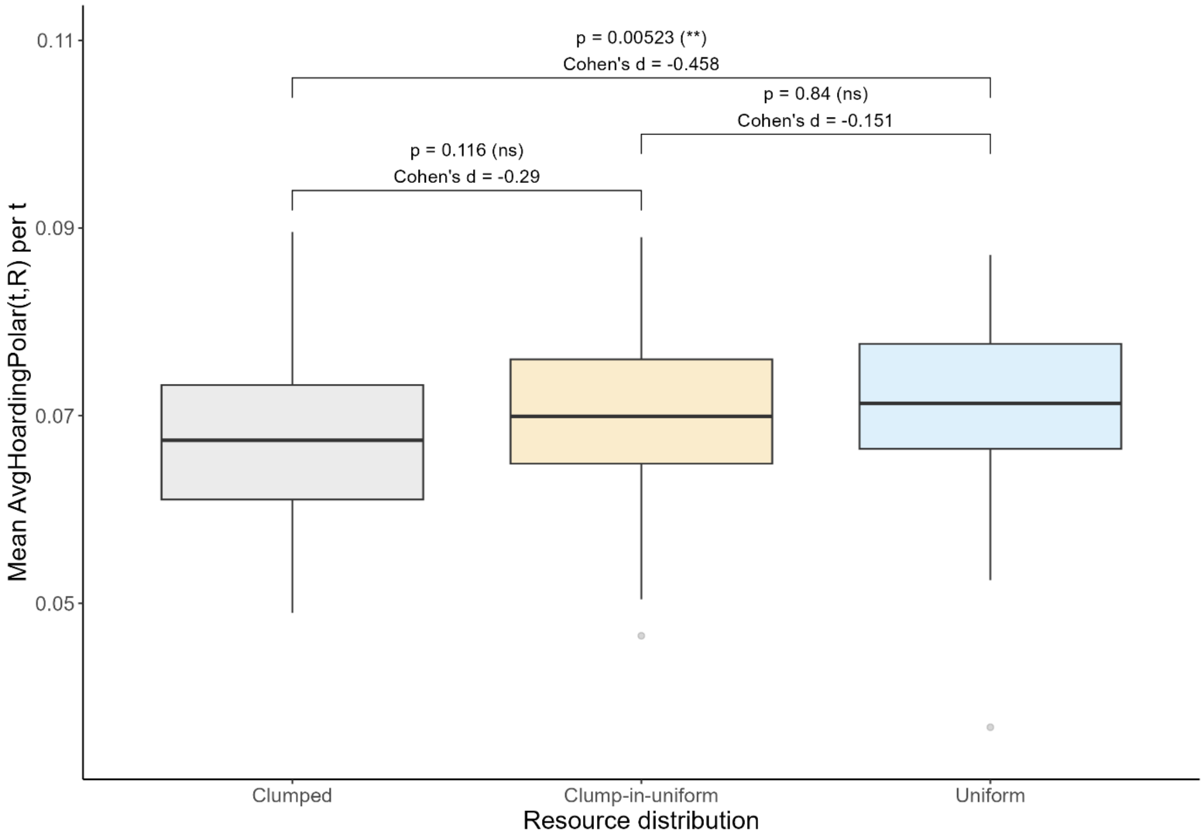

Figure 18. Boxplots of the mean $AvgHoardingPolar(t, R)$ per timestep, for three resource distributions and 100 iterations per distribution, along with the results (adjusted p-value with Bonferroni correction and Cohen's d) of the pairwise t-tests.

Differences between clumped and clump-in-uniform, and clump-in-uniform and uniform resource distributions were non-significant (adjusted p = 0.116 and 0.84, respectively).

A Shapiro-Wilk test indicates no deviation from normality (W = 0.991, p = 0.075), and visual inspection of the density and Q-Q plot of the residuals shows a normal distribution. A Levene's test indicates equal variance between distributions (F = 0.603, p = 0.548).

4.3 Hypothesis 3

4.3.1 Theorem 3a

The initial ANOVA indicates a significant difference in $AvgNonHoardingCcluster(t, R)$ between resource distributions (F(2, 297) = 22.6, p < 0.001). A pairwise t-test shows a significant difference between clumped and uniform resource distributions (adjusted p < 0.001) with large effect size (Cohen's d = 0.882) (Figure 19).

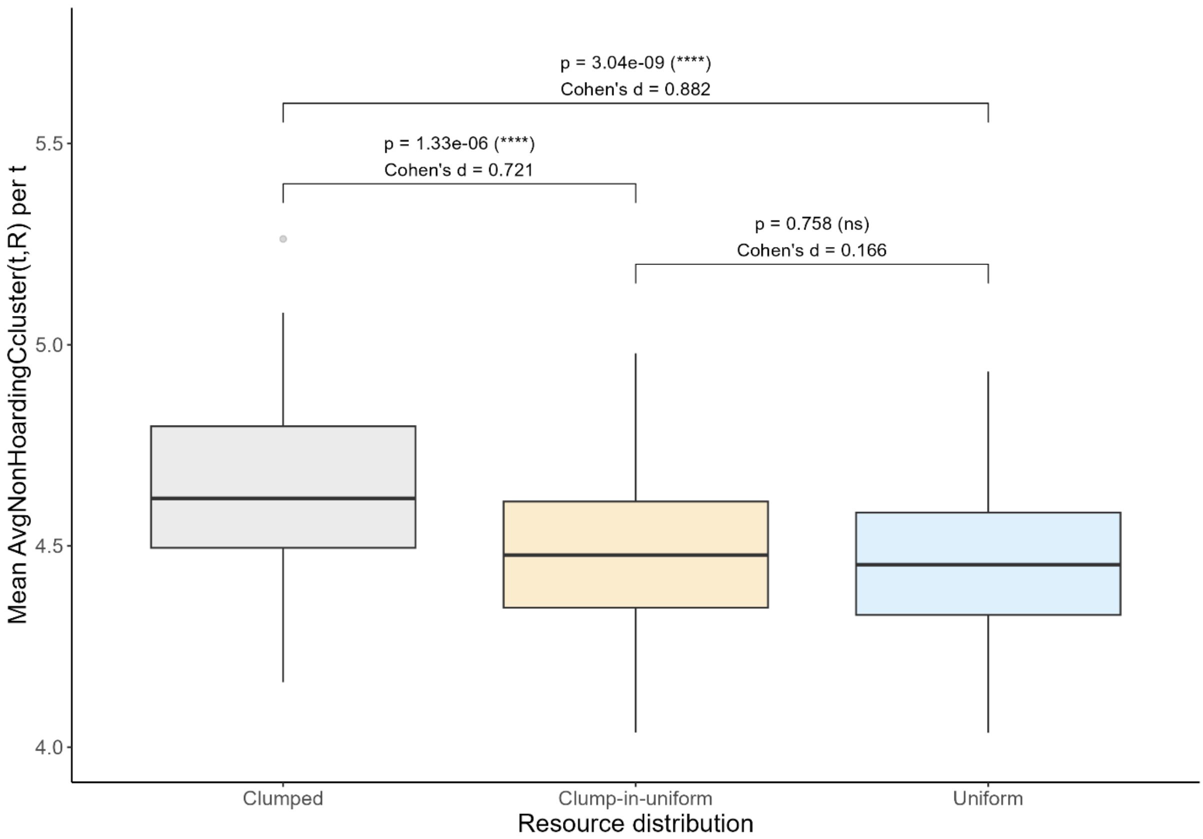

Figure 19. Boxplots of the mean $AvgNonHoardingCcluster(t, R)$ per timestep, for three resource distributions and 100 iterations per distribution, along with the results (adjusted p-value with Bonferroni correction and Cohen's d) of the pairwise t-tests.

A significant difference was also found between clumped and clump-in-uniform resource distributions (adjusted $p < 0.001$), with moderate effect size (Cohen's d = 0.721). Difference between clump-in-uniform and uniform resource distributions was non-significant (adjusted p = 0.758).

A Shapiro-Wilk test indicates no deviation from normality (W = 0.992, p = 0.091), and visual inspection of the density and Q-Q plot of the residuals shows a normal distribution. A Levene's test indicates equal variance between distributions (F = 0.441, p = 0.663).

4.3.2 Theorem 3b

The initial ANOVA indicates a significant difference in $AvgNonHoardingPolar(t, R)$ between resource distributions ($F(2, 297) = 7.871$, $p < 0.001$). A pairwise t-test shows a significant difference between clumped and uniform resource distributions (adjusted $p < 0.001$) with moderate effect size (Cohen's d = -0.553) (Figure 20).

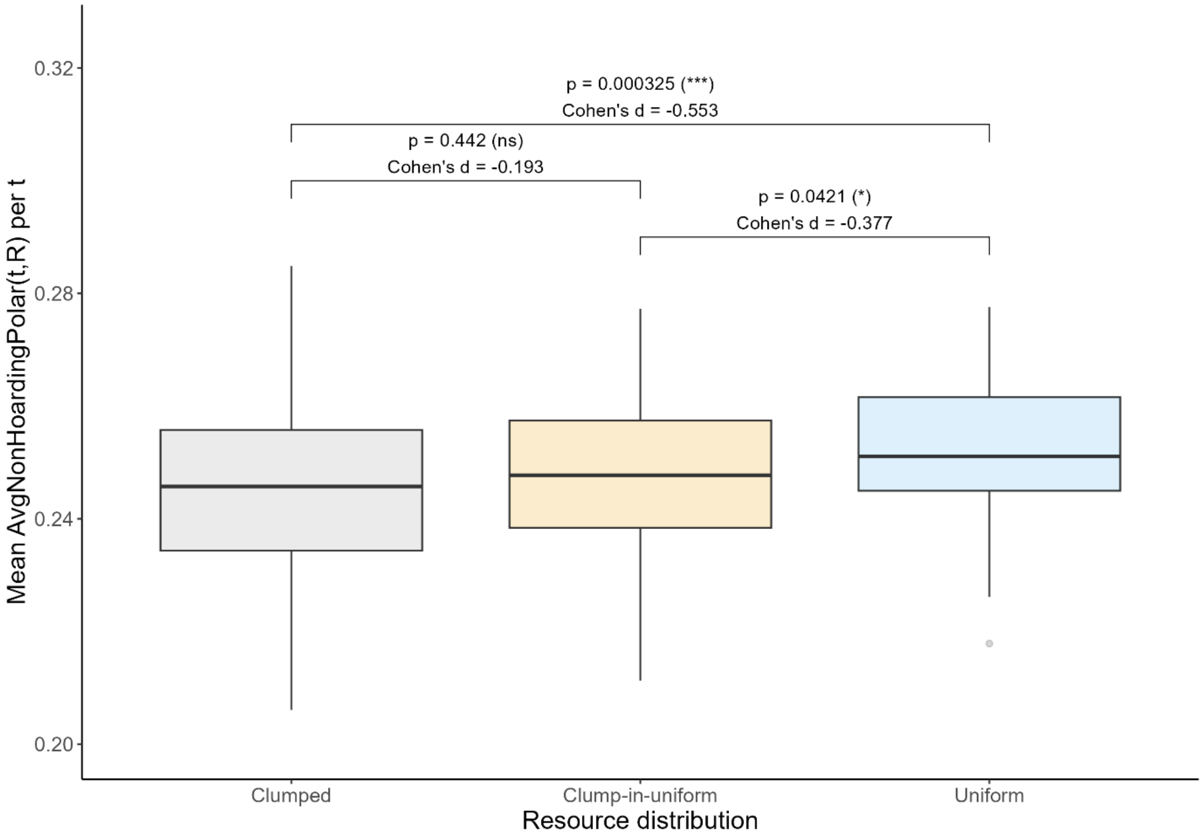

Figure 20. Boxplots of the mean $AvgNonHoardingPolar(t, R)$ per timestep, for three resource distributions and 100 iterations per distribution, along with the results (adjusted p-value with Bonferroni correction and Cohen's d) of the pairwise t-tests.

A significant difference was also found between clump-in-uniform and uniform resource distributions (adjusted p = 0.042), with small effect size (Cohen's d = -0.377). Difference between clumped and clump-in-uniform resource distributions was non-significant (adjusted p = 0.442).

Note that the effect has the opposite direction of what we hypothesized.

A Shapiro-Wilk test indicates no deviation from normality (W = 0.993, p = 0.173), and visual inspection of the density and Q-Q plot of the residuals shows a normal distribution. A Levene's test indicates unequal variance between distributions (F = 3.17, p = 0.043).

4.4 Hypothesis 4

4.4.1 Theorem 4a

The initial ANOVA indicates a significant difference in $HoardingEpisodes(t, R)$ between resource distributions (F(2, 297) = 3.577, p = 0.029). A pairwise t-test shows a significant difference between clumped and uniform resource distributions (adjusted p = 0.029), with small effect size (Cohen's d = 0.38) (Figure 21).

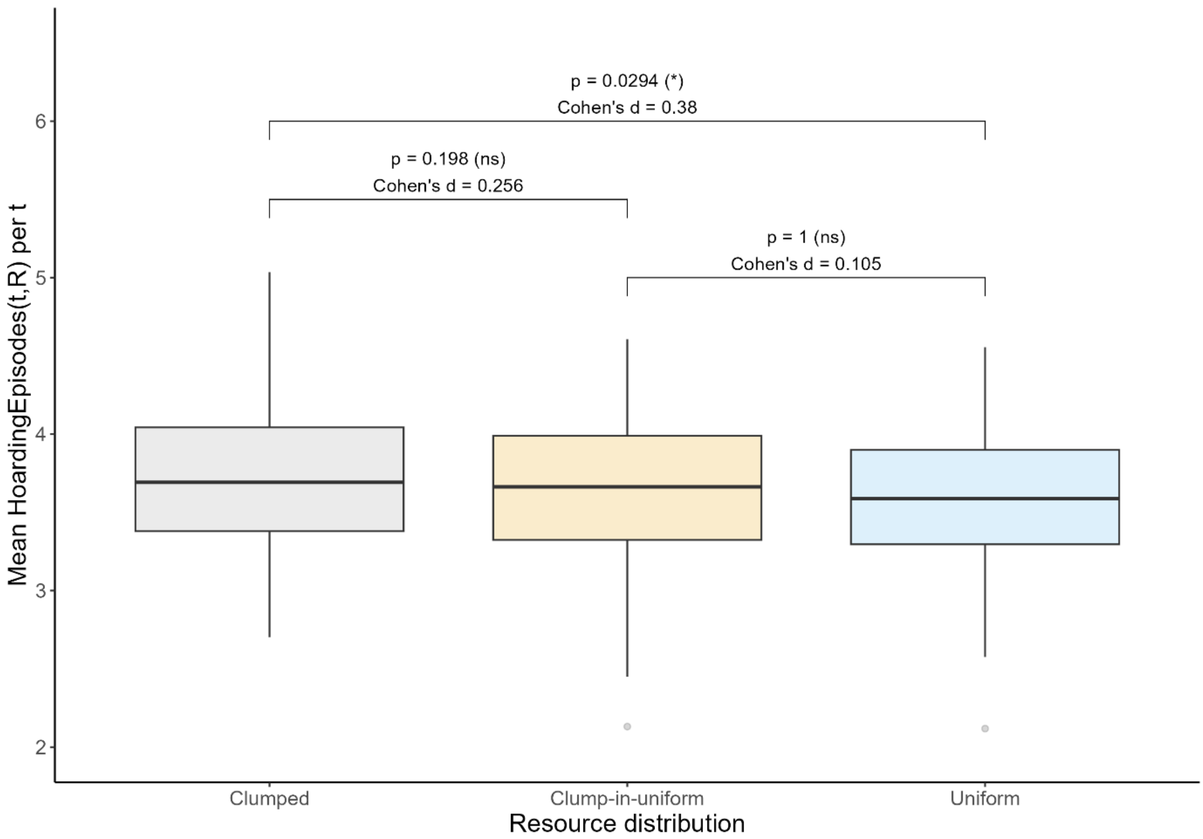

Figure 21. Boxplots of the mean $HoardingEpisodes(t, R)$ per timestep, for three resource distributions and 100 iterations per distribution, along with the results (adjusted p-value with Bonferroni correction and Cohen's d) of the pairwise t-tests.

Differences between clumped and clump-in-uniform, and clump-in-uniform and uniform resource distributions were non-significant (adjusted p = 0.198 and 0.105, respectively).

A Shapiro-Wilk test indicates no deviation from normality (W = 0.996, p = 0.753), and visual inspection of the density and Q-Q plot of the residuals shows a normal distribution. A Levene's test indicates equal variance between distributions (F = 0.142, p = 0.868).

4.4.2 Theorem 4b

After applying a reciprocal transformation ($\frac{1}{x}$), the initial ANOVA indicates no significant difference in $AvgHoardingAgents(t, R)$ between resource distributions (F(2, 297) = 1.193, p = 0.305). A pairwise t-test confirms this, showing no significant difference between any of the resource distributions (Figure 22).

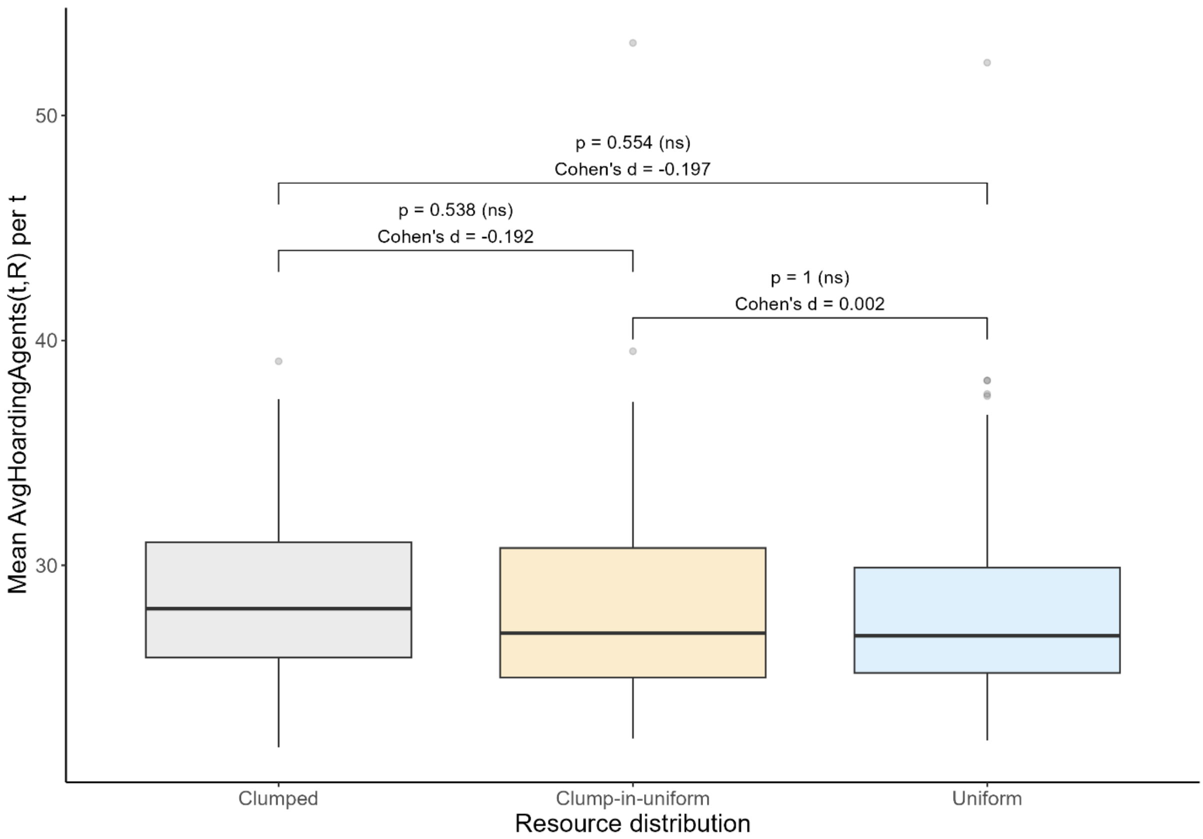

Figure 22. Boxplots of the mean $AvgHoardingAgents(t, R)$ per timestep, for three resource distributions and 100 iterations per distribution, along with the results (adjusted p-value with Bonferroni correction and Cohen's d) of the pairwise t-tests.

A Shapiro-Wilk test indicates a deviation from normality (W = 0.976, p < 0.001), and visual inspection of the density and Q-Q plot of the residuals confirms this (Figure 23). Given the robustness of ANOVA, we opt to continue with these results. These deviations are likely caused by outliers (see Figure 22).

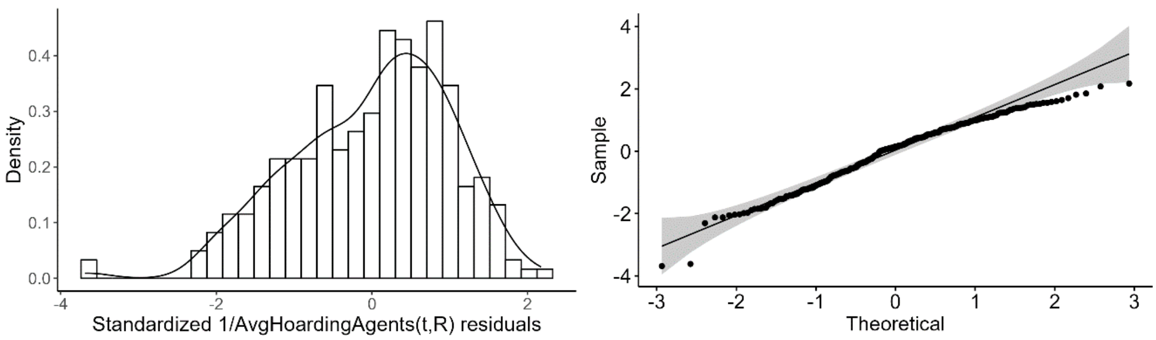

Figure 23. Density plot (left) and Q-Q plot (right) of the standardized residuals of the initial $AvgHoardingAgents(t, R)$ ANOVA, after reciprocal transformation.

A Levene's test indicates equal variance between distributions (F = 1.47, p = 0.232).

4.4.3 Theorem 4c

After applying a reciprocal transformation ($\frac{1}{x}$), the initial ANOVA indicates no significant difference in $AvgHoardingEnergy(t, R)$ between resource distributions (F(2, 297) = 2.305 p =

0.102). A pairwise t-test confirms this, showing no significant difference between any of the resource distributions (Figure 24).

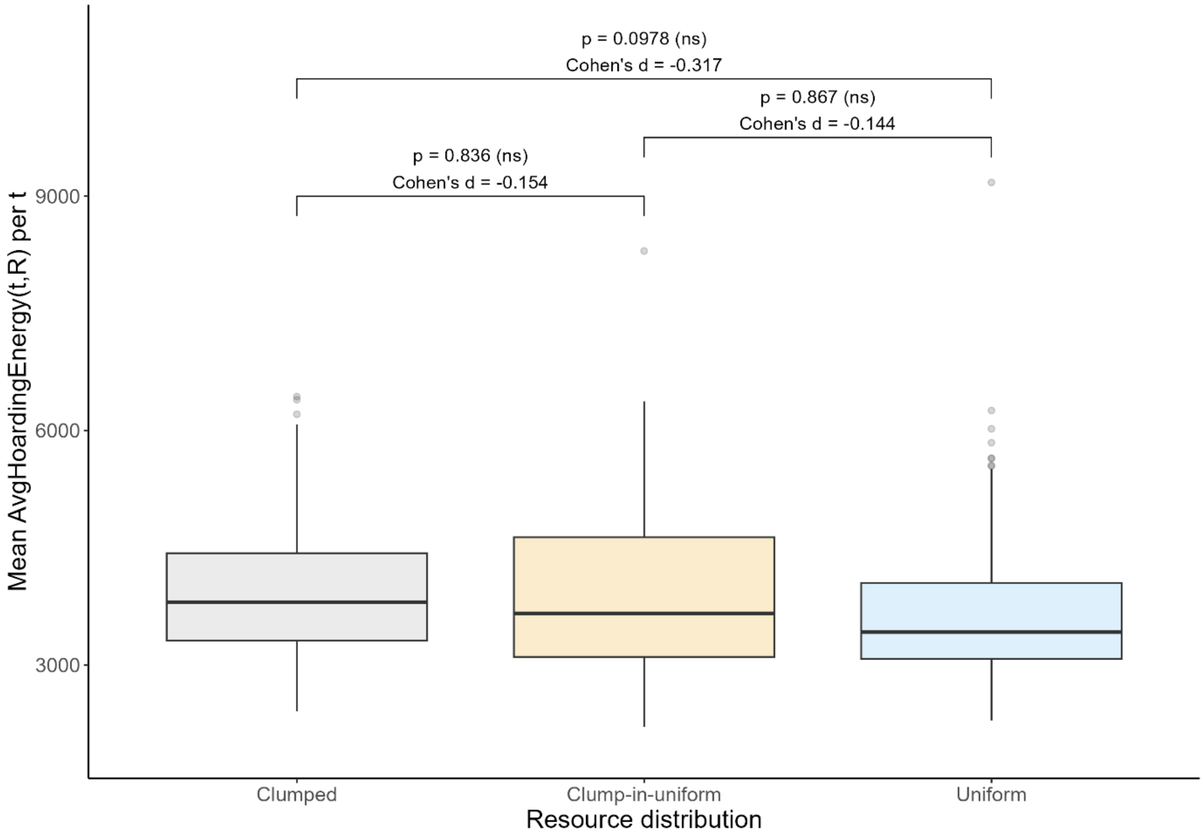

Figure 24. Boxplots of the mean $AvgHoardingEnergy(t, R)$ per timestep, for three resource distributions and 100 iterations per distribution, along with the results (adjusted p-value with Bonferroni correction and Cohen's d) of the pairwise t-tests.

A Shapiro-Wilk test indicates no deviation from normality (W = 0.996, p = 0.625), and visual inspection of the density and Q-Q plot of the residuals shows a normal distribution. A Levene's test indicates equal variance between distributions (F = 1.53, p = 0.217).

4.5 Hypothesis 5

The initial ANOVA indicates a significant difference in the Pearson correlation coefficients of $HoardingAgents(t, R)$ and $Cassort(t, R)$ between resource distributions (F(2, 297) = 26.08, p < 0.001). A pairwise t-test shows a significant difference between clumped and uniform resource distributions (adjusted p < 0.001) with large effect size (Cohen's d = 1.029) (Figure 25).

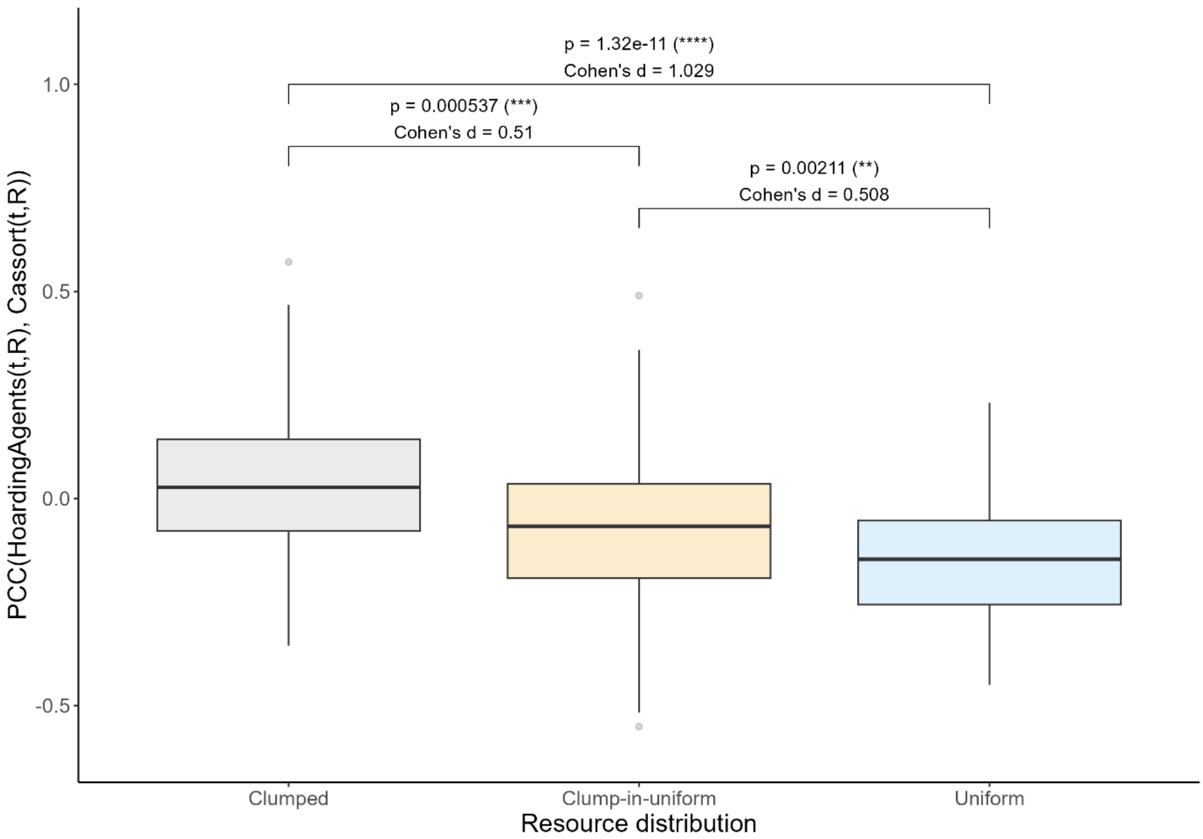

Figure 25. Boxplots of the mean Pearson correlation coefficient between $HoardingAgents(t, R)$ and $Cassort(t, r)$, per timestep, for three resource distributions and 100 iterations per distribution, along with the results (adjusted p-value with Bonferroni correction and Cohen's d) of the pairwise t-tests.

A significant difference was also found between clumped and clump-in-uniform resource distributions (adjusted $p < 0.001$) and clump-in-uniform and uniform resource distributions (adjusted $p = 0.002$), with moderate effect sizes (Cohen's $d = 0.510$ and 0.508, respectively).

A Shapiro-Wilk test indicates no deviation from normality ($W = 0.995$, $p = 0.391$), and visual inspection of the density and Q-Q plot of the residuals shows a normal distribution. A Levene's test indicates equal variance between distributions ($F = 1.10$, $p = 0.336$).

Chapter 5: Discussion

5.1 General conclusions

Based on the results, we conclude that there is a moderate difference in cooperator assortment between clumped and uniform resource distributions, but that the difference with the clump-in-uniform resource distribution is less clear (main hypothesis). We reject the second hypothesis stating that this is due to assortment on hoarding episodes is equal between resource distributions, because average polarization per hoarding episode is significantly lower in clumped than in uniform resource distributions. Similarly, we must reject the third hypothesis, because average polarization per non-hoarding episode is also significantly lower in clumped than in uniform resource distributions.

It seems then, that the differences in assortment between resource distributions are not caused by differences in polarization, but by differences in clustering which counteract the differences in polarization. Note that the assortment measure used in the analysis is based on both clustering and polarization (section *3.3.1.4 Clustering and polarization*).

Although we found no difference in the amount of agents or energy per hoarding episode between resource distributions, we did find a small but significant difference in the number of hoarding episodes between clumped and uniform resource distributions. We therefore cannot definitely conclude that the quantity of hoarding is equal between resource distributions (hypothesis 4), although it depends on how we define this quantity. We remark that insofar hoarding has an effect on assortment, the elements of interest are the agents of which assortment consists, not the energy or episodes (resources).

Finally, we conclude that the quality of hoarding is indeed highest in clumped resource distributions, next in clump-in-uniform resource distributions, and lowest in uniform resource distributions (hypothesis 5). The difference between clumped and uniform resource distributions was found to be large. However, it should be noted that the mean correlation coefficients lie close to or even below zero. This suggests that the amount of hoarding does not in fact increase assortment.

All in all, we conclude that the resource distribution does indeed affect the cooperator assortment in such a way that clumped resource distributions result in more assortment than uniform resource distributions, but we reject the hypothesis that this has to do with hoarding.

An analysis of differences in the cooperation proportion at uniform agent distribution $Cprop_{unif}(t, r)$ (equation 5) shows that the differences in assortment between resource distributions could be caused by the difference in uniform cooperator proportion. The initial ANOVA indicates a significant difference in $Cprop_{unif}(t, r)$ between resource distributions ($F(2, 297) = 18.02$, $p < 0.001$). A pairwise t-test shows a significant difference between clumped and uniform resource distributions (adjusted $p < 0.001$) with large effect size (Cohen's $d = 0.886$) (Figure 26).

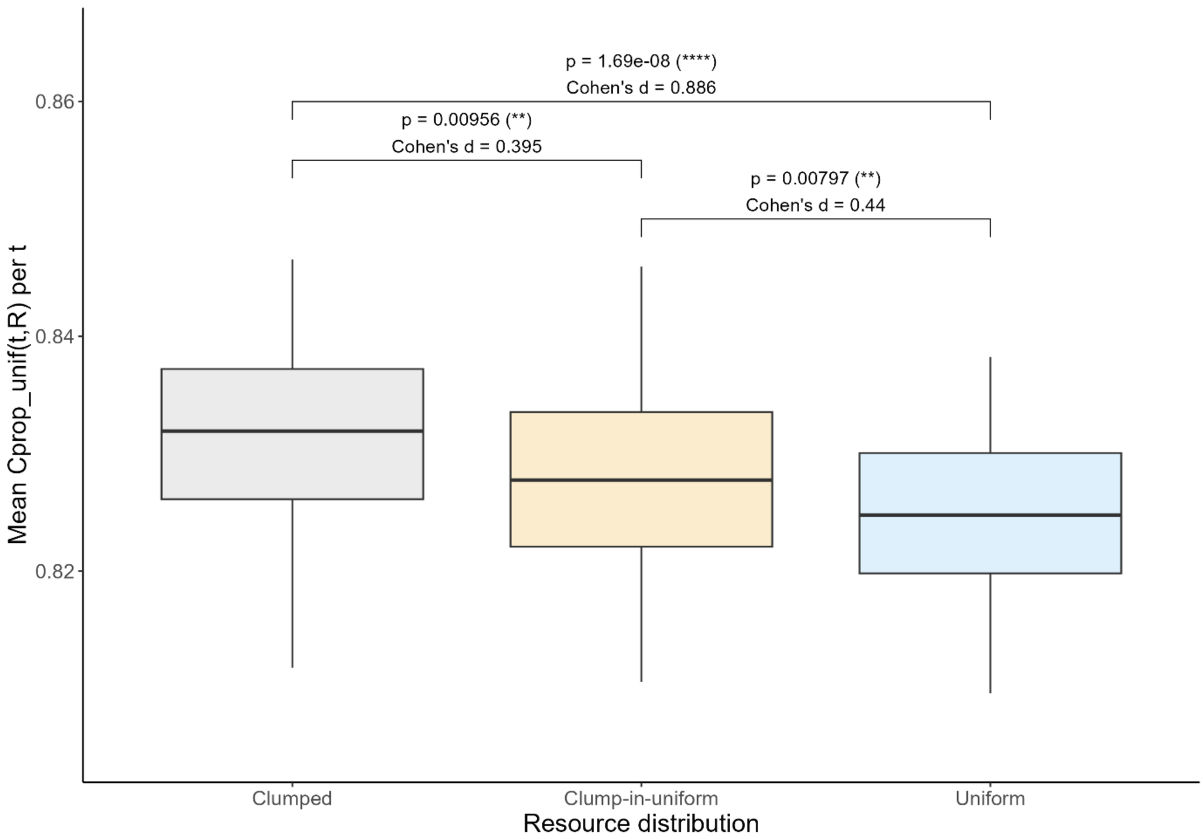

Figure 26. Boxplots of the mean $Cprop_{unif}(t, R)$ per timestep, for three resource distributions and 100 iterations per distribution, along with the results (adjusted p-value with Bonferroni correction and Cohen's d) of the pairwise t-tests.

A significant difference was also found between clumped and clump-in-uniform resource distributions (adjusted p = 0.010) as well as clump-in-uniform and uniform resource distributions (adjusted p = 0.008), but effect size was small (Cohen's d = 0.395 and 0.44, respectively).

A Shapiro-Wilk test indicates no deviation from normality (W = 0.992, p = 0.104), and visual inspection of the density and Q-Q plot of the residuals shows a normal distribution. A Levene's test indicates equal variance between distributions (F = 2.96, p = 0.053).

Note that $Cprop_{unif}(t, R)$ is the lower bound of $Cassort(t, R)$, and differences therein therefore have the potential to affect the results of the main hypothesis (see section *3.3.1.2 Assortment bounds*). One possible way to account for differences in $Cprop_{unif}(t, R)$ is to test for differences in cooperator assortment *relative* to these bounds. However, a reason *not* to account for these differences is that $Cprop_{unif}(t, R)$ is itself affected by the number of exploiting cooperators and defectors, which is affected by the number of cooperator and defector deaths. If on average the proportion of dead or exploring defectors is higher than the proportion of dead or exploring cooperators, the cooperator proportion at uniform agent distribution will increase. This is in itself evidence that the resource distribution affects the dynamics between these two types of agents, either through an unequal increase in exploration, or an unequal increase in deaths. Furthermore, deaths can only be the result of agent dynamics *on* resources, as agents do not lose energy while exploring (see section *3.1.2.3 Exploration*). A preliminary analysis of the number of defector deaths based on different payoff structures can be found in section *3.4.1 Sensitivity analysis* (Figure 10).

In our results, we have focused mostly on the differences between the clumped and the uniform resource distributions. More often than not, differences between the clump-in-uniform and uniform resource distributions where found to be not significant. In section *3.1.1.2 Resource distributions*, we stated that the goal of including the clump-in-uniform distribution in the analyses was to see if any differences between the distributions might be due to the presence of any clump, or due to heterogeneity in general. Comparing the distributions using a quantitative measure of heterogeneity, we found that $ResClust(RC) = 0.52$ for the clumped distribution, $ResClust(RCU) = 1.40$ for the clump-in-uniform distribution, and $ResClust(RU) = 1.78$ for the uniform distribution (Dry et al., 2012). The fact that the differences in this measure of heterogeneity are smaller between the clump-in-uniform and the uniform distribution than between the clump-in-uniform and the clumped distribution, might point towards the role of heterogeneity in and of itself being more important than the role of the presence of any clump.

5.2 Energy conservation

An unrealistic assumption of the model is that the inflow of energy in the system is infinite. A better model would keep the energy constant: the total inflow of energy should equal the total outflow. The total outflow per timestep is the energy spent on the cost of exploitation and metabolism by the agents. The total inflow is the energy transferred from the resources to all agents.

A potential solution could work with a common resource buffer, which all resources share. This resource buffer has an initial volume of energy, which during the model run is emptied via the energy that cooperators take from resources (the inflow), and replenished via the energy that agents spend on exploitation and their metabolism (the outflow). When this resource buffer is empty, all resources stop providing payoff simultaneously. This cap on total energy in the model forces all cooperators and defectors simultaneously to use their individual buffer energy. The pause of the total inflow will not take long because the total outflow of exploitation and metabolism of agents continues and refills the common resource buffer.

Such a model could be tuned by finding the total amount of energy in the initial setup - the individual agent buffers plus the common resource buffer - that together with the other tuning parameters leads to both reasonable buffer sizes and some assortment pattern. A monitor on the common resource buffer can then help find the minimal initial buffer sizes that just prevent the common resource buffer to run empty.

5.3 A fundamental, causal role of accidental buffers

Although excessive energy buffering in the form we have called “hoarding” is undesirable, energy buffers in itself are not problematic per se. They are a form of inequality, both with respect to other resources, as well as with respect to the other agents at those resources. Such inequality is the key emergent property in the Boltzmann wealth distribution model as well, where the random distribution of one unit of wealth between agents causes few agents to end up with most of the wealth (Dragulescu & Yakovenko, 2003). The payoff system in our model is essentially a random trading system of energy, with the stochasticity resulting from the random travel of agents to new resources. Like the Boltzmann model, our model starts out with a uniform distribution of wealth (energy), and inequality eventually emerges. Hoarding energy amounts to building a buffer so that the arrival of accidental defectors is not a problem, just like the accidental accumulation of wealth in Boltzmann’s model provides a buffer against setbacks too.

The effect of this energy buffering on assortment makes it difficult to study the causal effect of resource distribution heterogeneity. However, such buffering might not only be unavoidable, but even necessary for assortment to happen at all. Assortment can only happen if there is a difference in the *choice* or the *timing* between the movement of cooperators and defectors across resources. Because defectors can be safely assumed to *choose* resources with a lot of cooperators – if the capability of such a choice can be assumed at all – the effect that remains is *timing*. Differential timing between cooperators and defectors is a consequence of differential payoff, but buffering increases these differences further: the more buffering, the larger the time between departure of cooperators and defectors (see section *3.3.2 Hoarding*). Without buffering, cooperator departure would quickly be followed by defector departure, who would then end up at the same resources as the cooperators.

As stated in section *2.1 Explaining defection via the Resource Dispersion Hypothesis*, the RDH explains how resource heterogeneity can facilitate group living *without* providing any explicit benefits to cohabitation. This means that there must be other causes for group living *with* explicit benefits. Resource heterogeneity plays a similar facilitating role in our model as in the RDH, but we explicitly suggest differential timing between agent types as the cause of group formation: of assortment, in other words. Buffering of energy increases the gap in this timing, and resource heterogeneity plays a role in facilitating this.

5.4 Agent-level energy buffering

In the model's current form, at any given time most of the agents are on hoarding episodes, which are always emerging somewhere in the resource distribution. Averaged over time, the polarization on such a hoarding episode is low: although a resource going through a hoarding episode quickly gains in cooperators, it inevitably gains in defectors as well. However, this negates the element of *timing*, which causes cooperators to join the resource *before* defectors and *temporarily* raises the cooperator proportion and thus polarization (see section *3.3.2 Hoarding*). By definition, clustering is high too, meaning hoarding results in the temporary assortment of cooperators.

If agents spent a significant amount of their time on hoarding episodes, *and* a significant part of this time is characterized by positive assortment, then this has two consequences: (1) variation and selection are more likely to take place on hoarding episodes, and (2) due to the increased differences in timing, this selection will cause larger differences in cooperator and defector properties. Our model does not feature any variation or selection, but does claim that assortment emerges prior to the evolution of any real altruistic properties (see section *2.2 Minimal and fixed agent perspectives*). It therefore matters whether the emergent temporary assortment during hoarding episodes raises the likelihood of such evolution.

In our analyses, we considered the buffering of energy to be resource-level properties. Analysing energy buffering on the level of agents – and specifically, considering the differences between agent types – might shed light on how the sharing of individual buffers may be one of the first selected cooperator properties. Buffer sharing is present in nature too: for vampire bats, it is what allows some high-performing individuals to share their excess food with conspecifics in need (Di Tosto et al., 2007; Donepudi & Ramaswamy, 2018). Below a certain critical energy level, hungry vampire bats receive food from conspecifics with a larger food buffer.

We therefore suggest an improved model that (1) includes the conservation of energy in the system, (2) investigates the causal role of energy buffering, and (3) considers this energy buffering from the perspective of the agents, rather than the resources.

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