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The Evolution of Altruism in Spatially Structured Populations

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Abstract

The evolution of altruism in humans is still an unresolved puzzle. Helping other individuals is often kinship-based or reciprocal. Several examples show, however, that altruism goes beyond kinship and reciprocity and people are willing to support unrelated others even when this is at a cost and they receive nothing in exchange. Here we examine the evolution of this "pure" altruism with a focus on altruistic teaching. Teaching is modeled as a knowledge transfer which enhances the survival chances of the recipient, but reduces the reproductive efficiency of the provider. In an agent-based simulation we compare evolutionary success of genotypes that have willingness to teach with those who do not in two different scenarios: random matching of individuals and spatially structured populations. We show that if teaching ability is combined with an ability to learn and individuals encounter each other on a spatial proximity basis, altruistic teaching will attain evolutionary success in the population. Settlement of the population and accumulation of knowledge are emerging side-products of the evolution of altruism. In addition, in large populations our simple model also produces a counterintuitive result that increasing the value of knowledge keeps fewer altruists alive.

Keywords:
Altruism, Teaching, Knowledge Transfer, Spatially Structured Social Dilemmas

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Introduction

1.1

In the process of cultural transmission, individuals learn behaviors, values, and obtain information from other, not necessarily genetically related individuals (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Acerbi and Parisi 2006). People have a documented tendency to imitate others and to learn from others; that is they are receptive to cultural transmission provided by non-kin individuals (Simon 1990; Henrich and Gil-White 2001; Heyes 2001; Conte and Paolucci 2001; Conte 2002; Castro and Toro 2004). The capacity of imitation and docility provide fitness benefits and do not require the consent of the other individual. On the other hand, cultural transmission often requires an active role on the part of the provider that involves costs. This active role can be called teaching, or alternatively, instruction or social facilitation. Examples include many aspects of parenting, information sharing, knowledge transfer, or warning notifications. While a genetic imprinting of the capacity of learning from others can be explained with fitness benefits, it is more difficult to explain how teaching has been evolved (cf.Conte and Paolucci 2001; Tomasello, Kruger, and Ratner 1993).

1.2

A major part of teaching or instruction we observe has previously been claimed as kin-related. The efficient instruction of offspring increases the survival chances of the kin and thus ensures the spread and endurance of genetic material (Dawkins 1976). Kinship based teaching is altruistic but viable, as under the right conditions individuals will be more successful in spreading their genes by helping their kin than by acting in their own self-interest (Hamilton 1964a; 1964b; Kaplan and Hill 1985). Another major part of teaching is that it is part of an exchange or that it is fuelled by expectations and obligations that help will be reciprocated (Trivers 1971; Axelrod and Hamilton 1981).

1.3

There are several studies that highlight examples of "pure" altruism that are beyond kinship-based and reciprocal altruism (Henrich 2004; Gintis 2000; Bowles and Gintis 2003). The evolution of "pure" altruism, and in a specific context, the evolution of teaching behavior that benefits others and is not reciprocal, however, is an unresolved puzzle.

1.4

In a possible wider interpretation, teaching of non-kin can be seen as an exercise of social influence that prescribes a certain behavior that should be followed in society. There is often a direct incentive behind social influence, for instance, to spread a particular opinion, type of behavior, or value that establishes benefits for the provider.

1.5

From another point of view, voluntary teaching can be interpreted as a contribution to societal welfare or to the provision of public goods. In fact, teaching others at a certain cost is a contribution choice in a social dilemma that is not rational from an individual perspective and no teaching leads to a suboptimal social outcome. We know from the rich literature on social dilemmas that a contribution choice might oblige others to reciprocate indirectly with further contributions. This interpretation of teaching directs to research on indirect and of generalized reciprocity (Boyd and Richerson 1989; Yamagishi and Cook 1993; Bearman 1997). Existing research in this direction suggest that network forms of generalized reciprocity might provide a solution for the social dilemma (Yamagishi and Cook 1993). Some other theoretical models build on reputation and image scoring as solutions for similar social dilemmas (Raub and Weesie 1990; Rapoport, Diekmann and Franzen 1995; Nowak and Sigmund 1998; Wedekind and Milinski 2000).

1.6

In yet another perspective, teaching can be interpreted as the provision of help at a cost and might be contrasted with defective strategies of asking for help (de Vos and Zeggelink 1997). Simulation results show that providing help could be a successful strategy by preferring old helping partners (de Vos and Zeggelink 1997; de Vos, Smaniotto, and Elsas 2001; Back and Flache 2006). If agents differ with respect to their needs and they are spatially arranged such that they play support games with all their neighbors with a migration option afterwards, solidarity networks will emerge that are characterized by neediness class segregation (Hegselmann 1996; Flache and Hegselmann 1999). In short, these simulation models can explain how providing support evolves through mechanisms of partner selection.

1.7

We believe that this multidisciplinary variety of research has made significant contributions for understanding altruism, but is inadequate to explain why we encounter "pure" altruistic behavior and support of strangers in human societies that is not reciprocal in any way and is not conditional on previous actions. Teaching or providing help to a stranger is usually not determined by partner selection, but is influenced by a situational context and by the opportunity to interact or simply by proximity (cf.Becker 1976).

1.8

There are several studies that have followed this avenue and shown that a spatial structure of interaction promotes cooperation in social dilemmas (Nowak and May 1992; 1993; Hubermann and Glance 1993; Nowak, Bonhoeffer, and May 1994; Macy and Skvoretz 1998; Doebeli and Hauert 2005). The general conclusion of these studies is that cooperators are able to survive by forming clusters and harvesting the benefits of mutual cooperation that compensate them for the continuous exploitation by free riders. This conclusion overlaps with predictions of the theory of kin-selection (Hamilton 1964a; 1964b). When cooperators meet cooperators more than by chance and sufficiently often, they are able to survive. This is exactly what happens in a spatially structured population (Grafen 1985; Doebeli and Hauert 2005).

1.9

In this paper, we propose a simple model that can explain the evolution of unconditional altruism based on this idea. We will demonstrate that the key for the success of altruistic behavior lies in the conditions about the interaction structure. A similar conclusion to that of the "Hawks and Doves" model is reached (Maynard Smith and Price 1973); namely that altruistic traits are able to survive in the population; their success, however, becomes overwhelming when individuals meet each other on a basis of spatial proximity, which however is a realistic condition in the context of evolution. The particular original insight which is claimed for our study by comparison with the previous literature is that it examines side-products of the evolution of altruism and emergent properties related to the size of the population and the value of knowledge that is transferred.

The model

2.1

In this section we outline a simple model that conceptualizes teaching as a knowledge transfer that involves a cost for the provider. The model is very general, therefore sharing knowledge can be substituted to other forms of providing help. There is no exchange in the dyadic interaction and there is no indirect exchange. There is no bilateral or multilateral trade. Those who already possess the knowledge cannot gain anything more from a partner or from anyone else. They will merely decrease their reproductive chances by spending time disseminating their knowledge. There is no partner selection: teachers do not exclusively support their kin or preferred partners, but help those with whom they interact. No social elements of utility such as fairness or prosocial preferences are considered.

2.2

Dyadic interaction is modeled as follows. The population consists of agents who can be in two states: either having knowledge *K* or having no knowledge. An agent can attain knowledge from another agent who has *K* already and who is choosing to bear the costs *C* of teaching. The costs of teaching appear as opportunity costs that reduce the chance of reproduction, which is identical to how the costs of altruism were conceptualized in the model of Simon (1990). For the sake of simplicity, we assume that there is no direct cost in obtaining knowledge and compensation payments are not possible. In our simulation model, knowledge is utilized in a way that it increases survival chances. Hence, knowledge does not increase reproduction chances directly, just it prolongs the agent's life. The dyadic interaction between an agent with knowledge *K* and an agent without knowledge is represented in Figure 1.

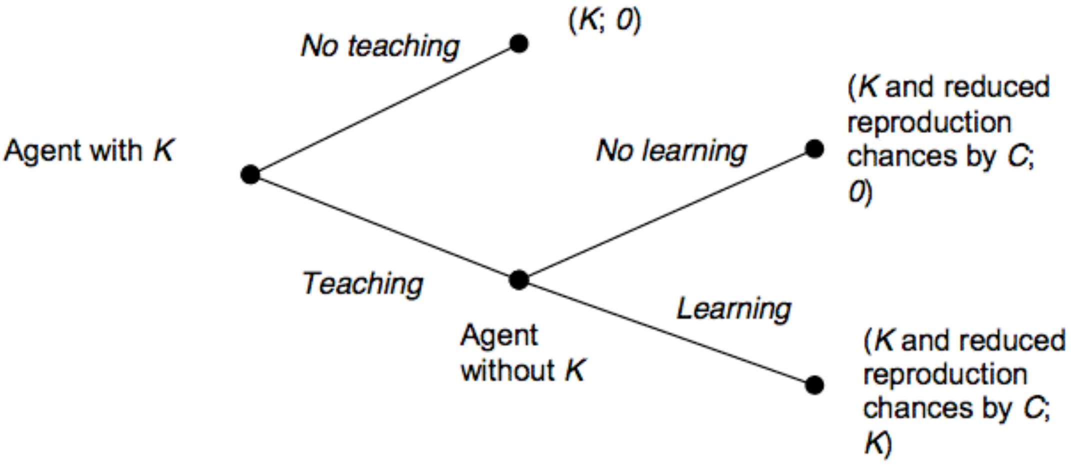

Figure 1. Dyadic Interaction of Teaching
K implies increased survival chances.

2.3

As Figure 1 shows, this is an asymmetric interaction in which no exchange or reciprocity is involved. The first agent decides to share knowledge *K* with the second agent or not. If he shares the knowledge, his reproduction chances are reduced by cost *C*. The second agent decides to accept this gift or not. An agent with *K* cannot get further knowledge or any additional benefits, and cannot lose the knowledge either. The first agent has a dominant strategy not to teach and in this case the second agent does not make any decision. There is no strategic interaction as the choice of the second agent does not have any effect on the first agent.

2.4

Individual strategies consist of two elements: whether to teach others or not and whether to learn from others or not. Individual inclinations of which elements of strategy they choose are genetically imprinted. Individual inclination for teaching is represented by the *T*-gene and responsiveness to teaching by the *L*-gene. Hence, there are only two genes and they both are either present or not. In this way, four possible combinations (genotypes) can be distinguished (*TL*, *T*, *L*, *0*), of which only the altruistic *TL*- and *T*-types are willing to teach others. Obviously, they are able to teach others if they have knowledge *K*. The *L*-gene is included in the analysis as the presence of learning assumed to be a precondition for the viability of teaching. Agents without the *L*-gene cannot gain knowledge from others, hence they can only acquire *K* with a small innovation probability. The naïve *T*-types, therefore, can make use of their altruistic trait only if they have attained knowledge by innovation. On the other hand, *TL*-types are able to acquire knowledge by learning from others as well as by innovation. *TL*-types are willing to pass on knowledge to others independently from how they have obtained knowledge, therefore their behavior cannot be described in terms of direct or indirect reciprocity. In general, teaching and learning are not dependent on previous behavior of the agents.

Simulation design

3.1

Our main hypothesis is that when individuals cannot differentiate between others based on kinship or on previous behavior, altruism in the form of teaching can still attain evolutionary success if individuals interact in a spatially structured population. In a spatially structured population altruistic teachers are willing to share their knowledge with everyone, but they are only able to do so in their proximity.

3.2

We will demonstrate the evolutionary success of non-naïve altruistic teaching by comparing two scenarios. In Scenario 1, matching is random and thus it reflects an unstructured society. In Scenario 2, interaction only takes place if the actors are within close spatial proximity.

3.3

In the simulations of spatially structured populations, agents are scattered in two-dimensional space.[1] Space is represented by a grid with boundaries, but this assumption can be easily relaxed. We do not make restrictions on the proportions of genotypes in the initial population and on their initial spatial distribution. In most of our examples, agents at the start are randomly scattered in the grid with a uniform distribution and each agent is assigned with 0.25 probability to one of the four genotypes.

3.4

Agents do not live forever: the probability of individual survival after each round (year) is determined stochastically by the baseline survival parameter. This is the same for all agents without knowledge. The value of knowledge *K* appears in the form of increased survival chances. For instance, the survival of an agent who has no knowledge after the first year is determined by the baseline survival parameter. If the same agent obtains knowledge in the second year, his survival chances after the second year are grown from the baseline rate to the increased rate. Survival probabilities can be translated into average life-expectancy at birth. For the sake of easier interpretation, we will report these parameters as (expected) baseline life-span and extra life-span. We will present results of simulations, where the population size is fixed, hence the number of offspring is equal to the number of agents who die in the given year.

3.5

Agents start with no knowledge at all. In each year, agents are selected in an asynchronous sequence. They can obtain knowledge *K* by a small innovation probability in each year. The innovation probability is the same for all genotypes. Once an agent acquired knowledge, he will not forget it before he dies. When an agent has knowledge *K* and also the teaching gene, he searches for a partner agent without *K* in his bounded proximity. The probability of a match is inversely proportional to the square of distance. The pseudo-code of interaction within one year can be found in the Appendix.

3.6

We introduce a stochastic parameter for teaching that indicates how often the teaching gene is expressed in the phenotype. It is the proportion of agents trying to teach among agents with the *T*-gene. Note that we do not introduce a stochastic parameter for learning: if a partner is selected who has the *L*-gene but no knowledge, *K* is shared and the survival chances of the partner are increased.

3.7

After each year, some agents die and new agents are born in a number such that population size remains constant. The genotype of the dying agents does not influence which types of agents are born. All living agents have equal reproduction chances, except that the cost of teaching (*C*) appears as an opportunity cost: the chance of reproduction is lower for those agents who teach in the given year. Genes are inherited with a certain mutation rate. Offspring are born within the bounded proximity of the breeding agent at a random location. This is obviously unimportant in Scenario 1 and of crucial importance in proximity based interaction. In Scenario 2, we have a "viscous" population in which reproduction and interaction takes place locally (cf.Hamilton 1964a; Grafen 1985; Axelrod, Hammond and Grafen 2004).

3.8

In the simulations reported in the next section, we used the following parameter values. In small populations, the number of agents is fixed to 100. In all simulations that are reported, we fixed the mutation rate to 0.1%; the innovation rate to 0.1%; the breeding range to a circle with a radius of 20 pixels; the teaching range to 32 pixels; and the entire grid size to 256 by 256 pixels. In all simulations reported, a *T*-gene calls for teaching with a probability of 0.5 and teaching decreases breeding chances by 10% (*C*). Unless otherwise noted, the expected life-span of agents is 2 years and *K* adds 2 years to this. Hence, knowledge is really valuable and doubles the lifetime of an agent. Knowledge, though, has no direct value for reproduction; but a prolonged life provides an indirect value. Changing some of these parameter values unilaterally have decisive consequences for model predictions, but most of these effects are self-explanatory. We will discuss some of these effects later.

Results

The evolution of altruistic teaching in small populations

4.1

We observe qualitatively different dynamics in our simulations in small and in large populations. First we discuss results in small populations. At low mutation rates, we observe the evolution of an overwhelming majority of a single genotype for both scenarios. These "regimes" where almost the entire population has the same genes last long and are separated by short transitions.

4.2

In principle, if there is no knowledge, population ratios tend not to change as the births of offspring are proportional to ratios in the old generation. Changes in the population ratios occur due to random processes. This kind of dynamic can be illustrated by modeling changes in the population ratios as a bounded random walk. When a genotype is represented by few agents only, there is a pressure towards extinction, since the number of offspring in a given year is restricted by population size. Since this applies to all the four ratios, in the long run one genotype will attain a 100% share in small populations. This is a general qualitative attribute of the simulations in small populations, irrespective of the initial conditions. It does not matter how genotypes are distributed, how much knowledge is there at start or how interaction takes place: one genotype gains dominance over time. Increasing the share of one genotype in the initial population also increases its chance to become first to gain dominance. Once a genotype obtained dominance, it keeps its 100% share relatively long until it is broken down by a transition (see Figure 2). These transitions occur necessarily for all regimes due to the random elements of the model. The questions of how do transitions occur and how long different regimes last are important for determining the success of different genotypes.

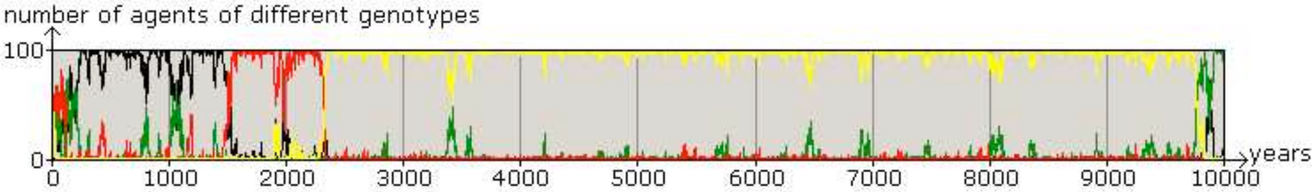

Figure 2. 10000 years of Business as Usual: Success of Altruistic Teachers
Scenario 2, the four genotypes (*TL*: yellow, *L*: green, *T*: red, and *0*: black) are approximately equally represented in the initial population of 100 agents. *0*-types (black) are invaded by *T*-types (red) in times without knowledge. This is followed by an invasion of *TL*-types (yellow) and accumulation of knowledge, with the invasion of *L*-types(green) before year 10000. Meanwhile there are a lot of unsuccessful bids for power. Altruistic teachers have an overwhelming majority significantly longer than others.
In this example: mutation rate: 0.1%; innovation rate: 0.1%; breeding range: 20 pixels; teaching range: 32 pixels; a T-gene calls for teaching with a probability of 0.5 and teaching decreases breeding chances by 10%. The domination of yellows (*TL*) is robust for changes in the auxiliary parameter values.

4.3

Transitions do not occur with the same probability between different regimes. Transitions start after a mutant appears in the homogeneous regime and starts to propagate. Double mutations are unlikely and therefore opposite genotypes (*TL* and *0*; *T* and *L*) do not start to spread in a homogeneous population. As a consequence, transitions between opposite genotypes occur rarely. Besides this natural difference, there is also a difference between transition probabilities due to the role of knowledge and teaching. Only *TL*-regimes can have the characteristic that they preserve knowledge in the population after it was acquired. If knowledge is preserved in the population, teachers without the ability of learning are unable to benefit from the knowledge of *TL*-types, while learners without the capacity of teaching have reproduction advantages. Therefore *T*-invaders will be less successful than *L*-invaders in a *TL*-population. This has the consequence that the transition from a *TL*-regime to a *T*-regime is much less likely than a transition to an *L*-regime. Furthermore, even if *T*-types acquire knowledge by innovation, their breeding chances are decreased by the act of teaching, while they cannot transmit knowledge to their own offspring. This explains why in both scenarios, the evolution of regimes of the *T*-genotype is the least likely. *L*-types can successfully exploit and invade the *TL*-population in both scenarios (cf. Figure 3). They benefit from teaching and as they do not teach themselves, they start to breed more efficiently. Some knowledge is preserved only while there are some *TL*-types around.

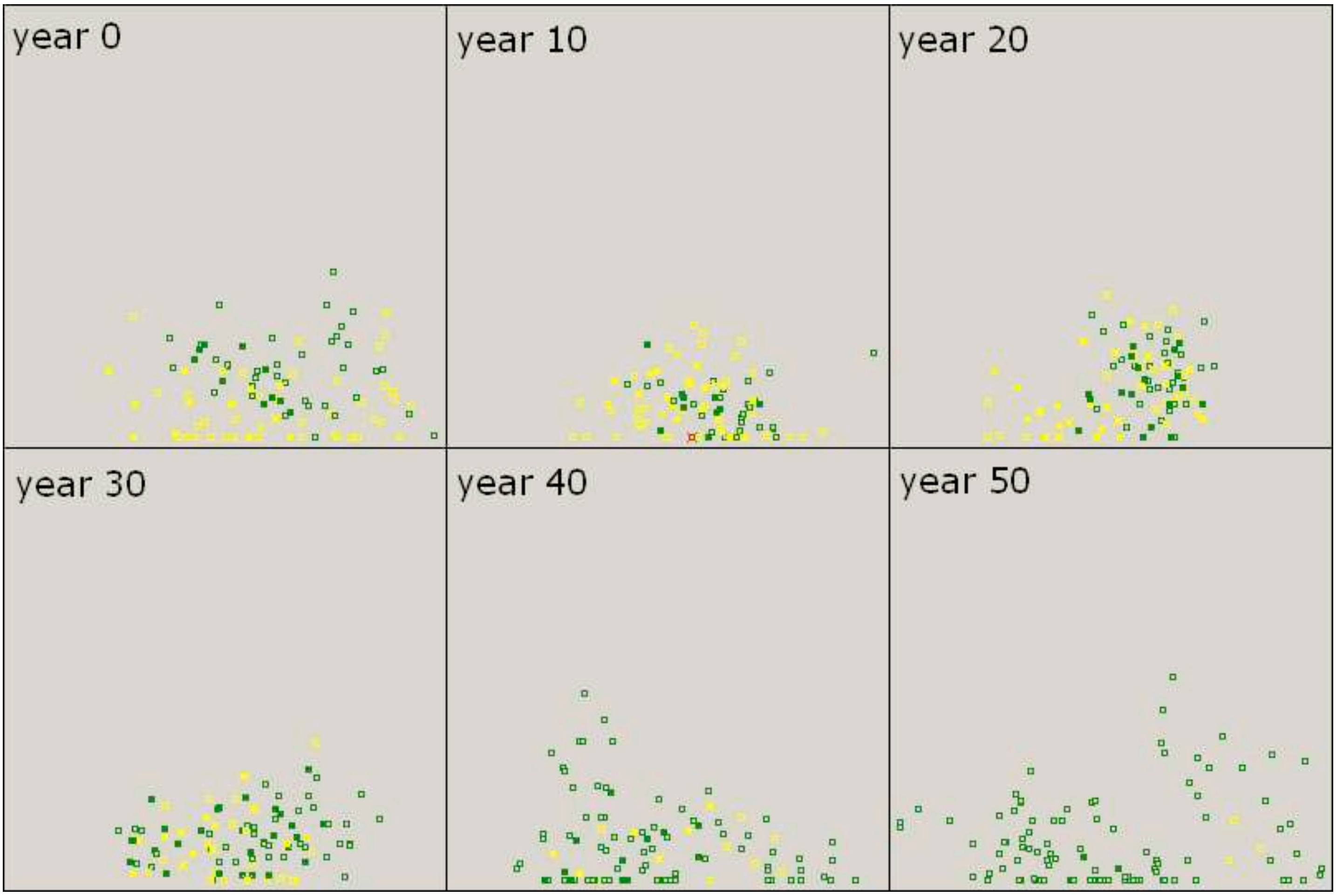

Figure 3. Triumph of Free Riders
Filled squares represent agents with knowledge. Green agents (*L*) exploit yellows (*TL*) gradually (years 0-30). As *TL*-types diminish, knowledge among greens becomes scarce (year 40). By the end, *L*-types attain an overwhelming success, but have no knowledge (year 50).
Scenario 2, the initial population consists of approximately the same number of *TL*-types and *L*-types. Parameter values are the same as before.

4.4

At a relatively low mutation rate in a small population, in both scenarios, uniform regimes of genotypes alternate with each other. The success of different genotypes in these circumstances can be determined by the length of regimes. With random matching and significant teaching costs, the total length of *TL* regimes is not longer than of other genotypes.[2] The length is measured in terms of effective generations and not in years as living longer is related to having knowledge and this would give a biased indication of the viability of a genotype. Even under Scenario 1 with random matching, however, altruists might be the overwhelming majority for a certain time. The explanation lies in the fact that in a population without knowledge, there are no costs of teaching either, hence all genotypes can gain dominance equally likely. The lack of knowledge explains also why we do not see a clear evolutionary advantage of the capacity of learning.

4.5

In contrast, altruistic *TL*-types attain an overwhelming success in a spatially structured population.[3] The rule of the *TL*-types occurs more frequently and lasts longer than regimes of other types (cf. Figure 2).[4] There are more reasons why a spatial structure helps the evolutionary success of non-naïve altruistic teaching besides the fact that self-sustaining *TL*-regimes can only be exploited by *L*-types and other regimes are sensitive to mutations in both alleles (*T*, *L*). While one genotype has an overwhelming majority, other genotypes make several attempts to take over. A concentration of newcomers that is already sufficient for successful invasion is smaller for *TL*-types than for others, as they are able to transfer knowledge to their neighborhood. Since both interaction and reproduction are local, after altruists start to propagate, they are surrounded mostly by other altruists. Therefore the benefits of altruistic teaching go mainly to the altruistic teachers themselves. This is a segmentation effect that supports the viability of social traits also in different contexts (Axelrod and Hamilton 1981; Becker 1976; Bowles and Gintis 1998; Flache 2004; Doebeli and Hauert 2005). The success after a smaller concentration also explains why the *TL*-types are the most likely to gain overwhelming success from a randomly mixed initial population (cf. Figure 4).

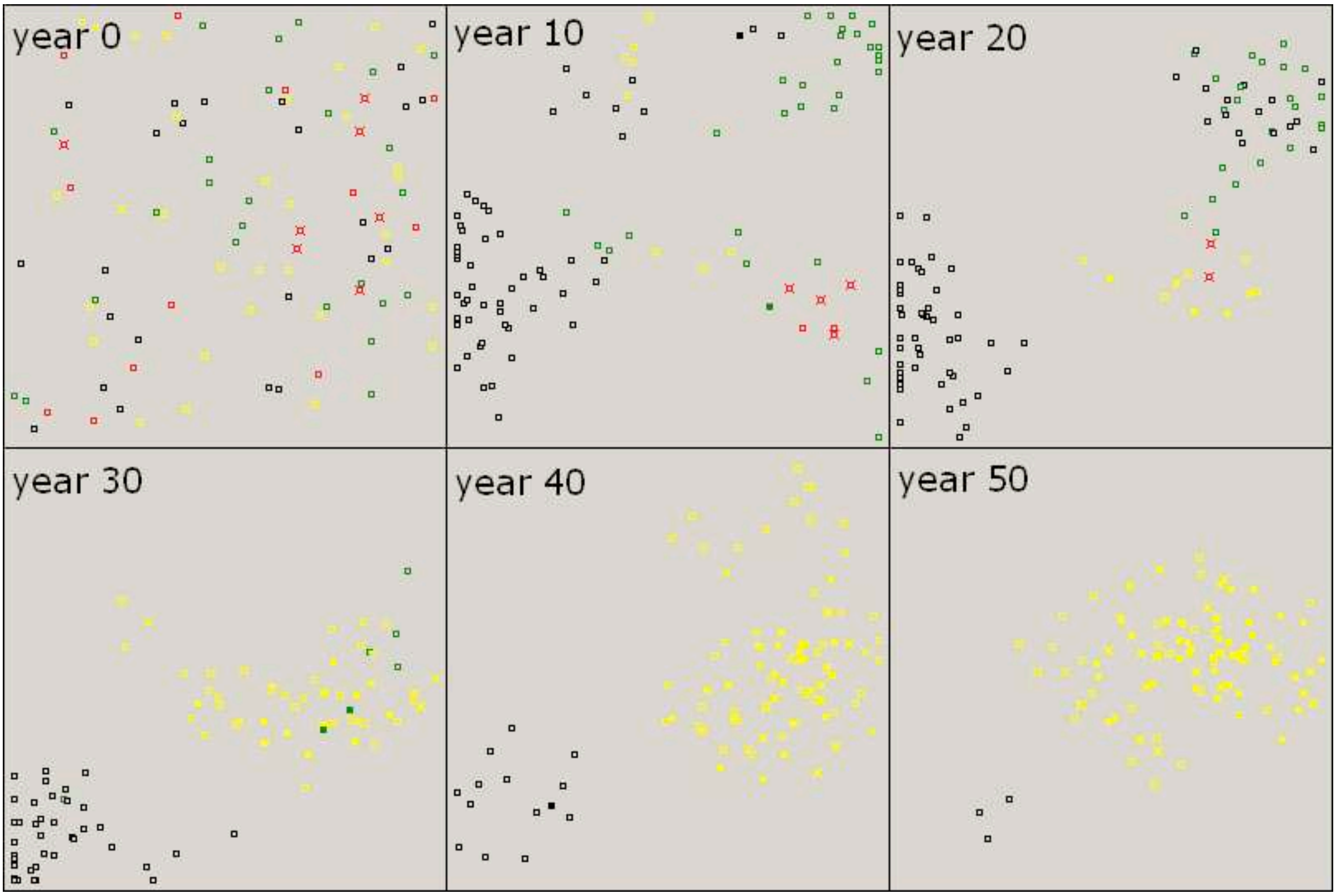

Figure 4. Knowledge is Power
Starting from a random mix of agents (year 0), genotypes become segregated, since new agents are born close to their parents (year 10). Knowledge appears among yellows (*TL*) due to innovation and teaching, while greens (*L*) are mixed with blacks (*0*) (year 20). Although some greens acquire knowledge in year 30, they die out (year 40) and yellows prevail (year 50).
Parameter values are the same as before.

Settlement emerges

4.6

The success of altruistic teaching leads to an emergent phenomenon: to the settlement of agents and to the accumulation of knowledge. This can be explained as follows. Spatial concentration of agents is mainly the result of the rule that offspring are born around the breeding agents. If there is no knowledge in the population, evolution does not select agents based on their spatial location as there are no advantageous places for newborns. As a consequence, agents are moving in herds in a random manner. However, if altruistic parents have already acquired knowledge, they live longer and the offspring as well as free riders take advantage of settling close to the old generation. The result is a concentrated and settled population. High population density makes it possible to collect knowledge efficiently and maintain a knowledge pool that profits the entire community.

Results: Large Populations

4.7

Simulation results are sensitive to changes in the total population size. First, a larger population in the same space means higher density, which might have an effect in Scenario 2. Second, a larger total population means that genotypes with a smaller population share can also safely reproduce and are not subject to easy extinction.

4.8

If we increase the total population size from 100 agents to 200 agents, the success of the *TL*-type measured in length of regimes in a spatially structured setting becomes more apparent (see upper part of Figure 5). In a large population, however, the steady states of pure regimes give place to mixed equilibria with *TL*- and *L*-types present (lower part of Figure 5). The larger the population, the less the variation is in the actual proportions of *TL*- and *L*-types. This also means that the overwhelming dominance of altruistic *TL*-types is less frequent in larger populations (Figure 6).

4.9

Homogeneous regimes do not evolve in large populations, as reproduction leads to extinction at more extreme proportions. The random walk of population ratios do not reach the boundaries for *TL*- and *L*-types. In these neutral circumstances what matters in fact is knowledge - and as knowledge is around, the capacity to learn. As Figure 5 shows, *T*- and *0*-types are occasionally able to achieve dominance at population sizes of 200 and 400, but this is much less likely than in a population of 100. In larger populations, after acquiring knowledge, *TL*- and *L*-type agents crowd out *T*- and *0*-types, since the latter do not utilize knowledge. In short, our simulations show qualitatively different dynamics for small and large populations. While in small populations, different regimes alternate each other with a clear dominance of altruistic *TL*-types in Scenario 2, in large populations *TL*-types and *L*-types are both represented and other types are disappearing.

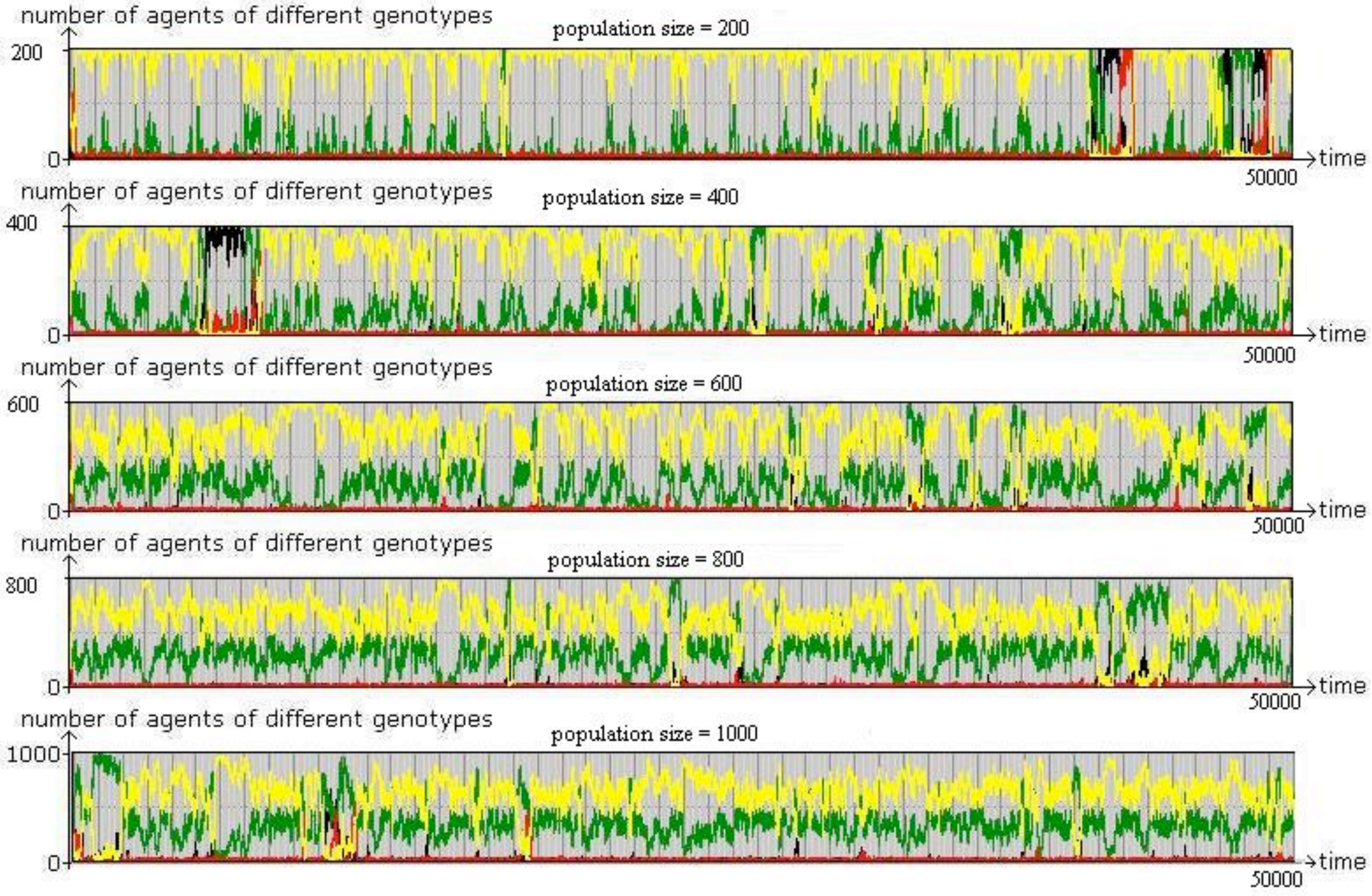

Figure 5. The Effect of Population Size
Proximity based interaction, starting from a random mix of agents (year 0).
Parameter values are the same as before with varying population size.

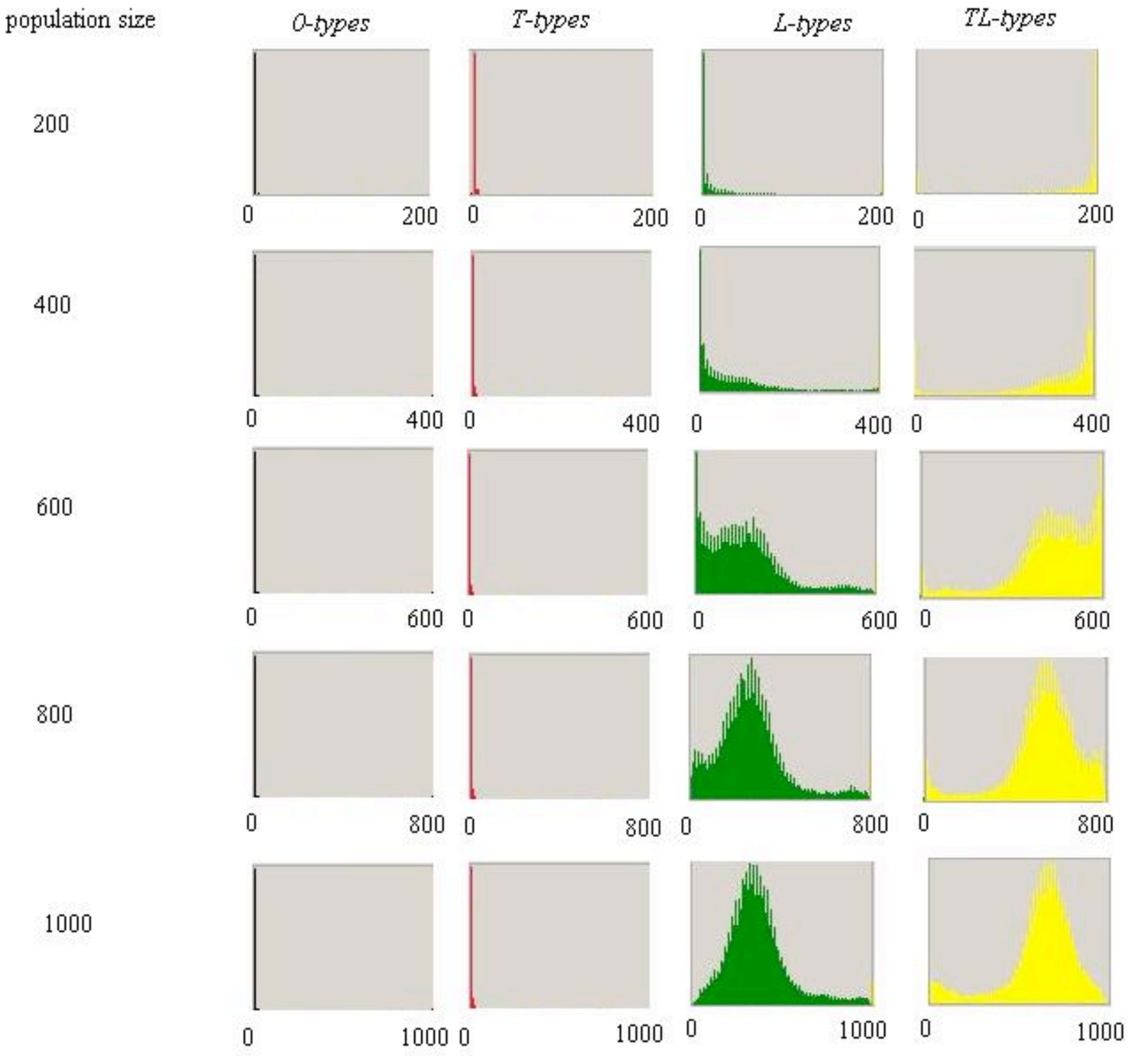

Figure 6. Probabilities of Different Proportional Distributions of Agents by Population Size
Number of agents are on the horizontal axis ranging from 0 to population size and probabilities (frequencies) are on the vertical axis. Proximity based interaction, starting from a random mix of agents (year 0), for the same runs as in Figure 5.
Parameter values are the same as before with varying population size.

4.10

We observe substantial differences between the scenarios of random and local interaction also in large populations. In case of random matching, *L*-types prevail among the population (Figure 7). Teachers try to invade from time to time, but they usually die out due to overexploitation, which is the main consequence of random interactions. Unsuccessful invasions provide free riders with knowledge and keep them in majority.

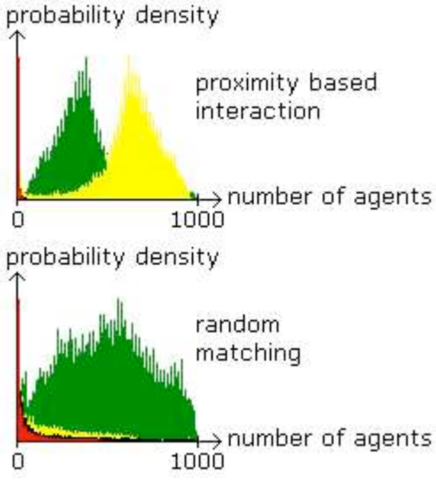

Figure 7. Mixed Equilibrium in a Large Population
Proximity based interaction in a spatially structured population (above) is a key for success of the *TL*-types (yellow) also in a large population. They have to share the space with *L*-types (green). *L*-types gain success among the population in case of random matching (below).

Parameter values are the same as before except that there are 1000 agents.

4.11

In a spatially structured population, *TL*-types come to power with a large store of knowledge among them, but free rider learners (*L*) will continuously exploit them. Meanwhile, the crowding out of *0*- and *T*-types takes place. As *L*-types procreate more efficiently (without teaching costs), their population ratio increases. This leads to the decrease of the proportion of *TL*-types and more importantly of knowledge. The latter has a negative impact on *L*-types (shortening their life-span), which in turn helps *TL*-types regaining a higher ratio (cf. Figure 8). These two opposite forces keep proportions of these types within certain bounds and the result is a mixed stochastic equilibrium (cf. Figure 9). Similar to the hawks and doves dilemma, where equilibrium proportions in the population depend on the payoff parameters (cf.Maynard Smith and Price 1973; Frank 2003); in our model, equilibrium proportions depend on parameters *K* and *C* and on interaction possibilities. Meanwhile in a moderately large population *TL*-types are in the majority, free riders have a higher proportion in case the population is so dense that altruistic teachers cannot escape being exploited.

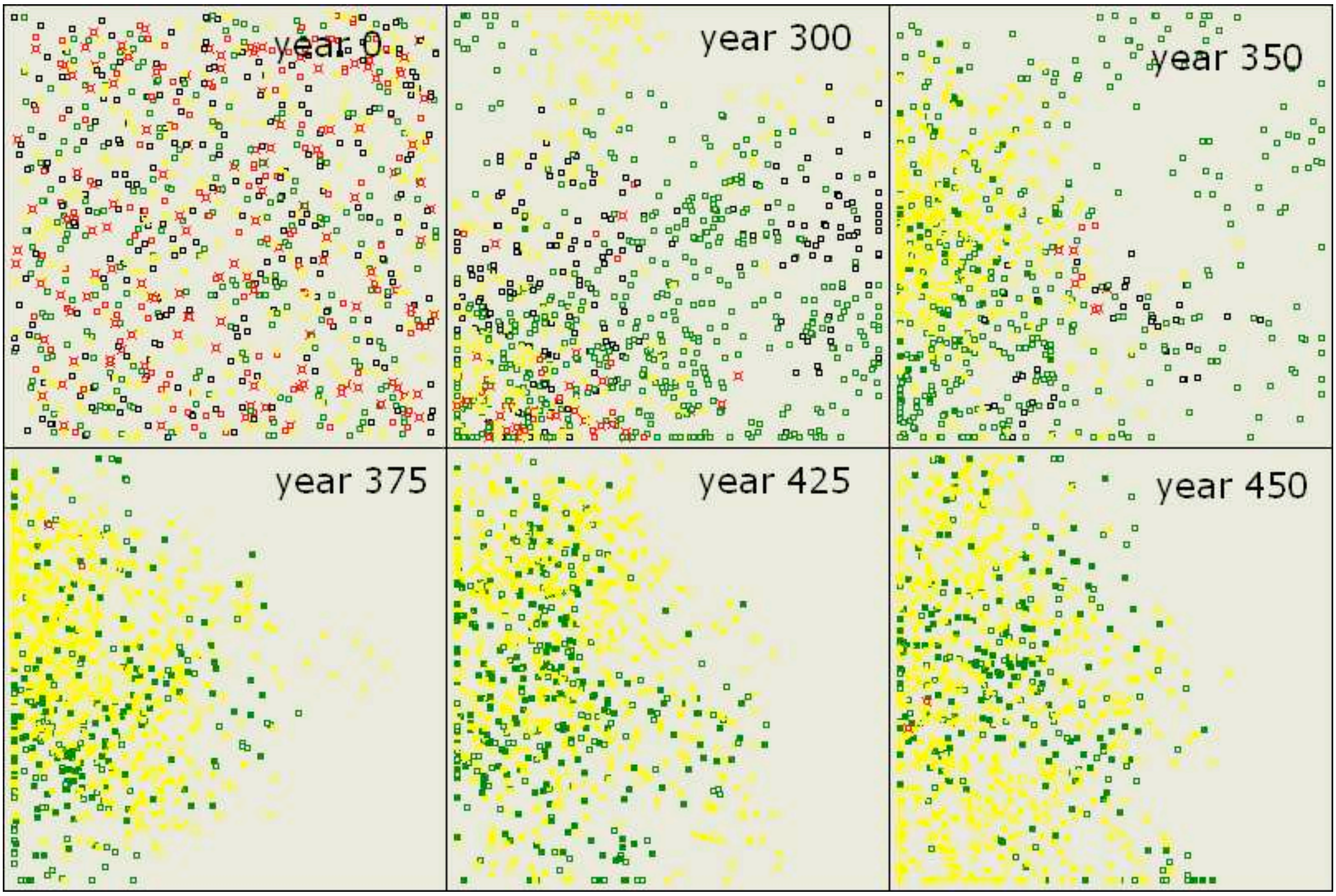

Figure 8. Exploitation and Recovery of Altruistic Teachers
After a random start (year 0) and random processes, yellows (*TL*) attain success and accumulate knowledge (year 350-375). Greens (*L*) are efficient in free riding (year 425), but altruistic teachers recover by establishing centers of knowledge at new locations (year 450).
Parameter values are the same as before except population size (1000).

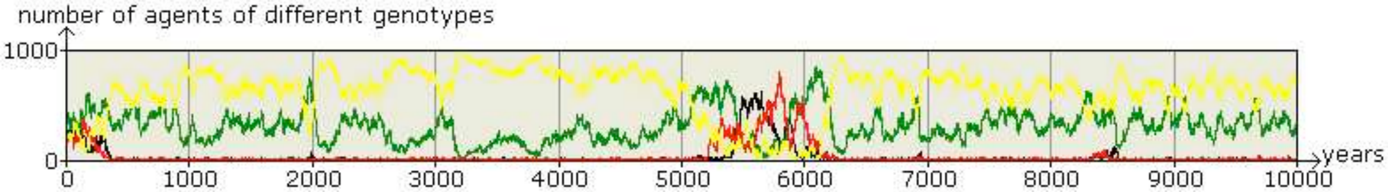

Figure 9. Genotypes Live Side by Side in Large Populations
Increasing population size results in the coexistence of yellows (*TL*) and greens (*L*).
This example is for the simulation run represented in Figure 8.

4.12

A paradox emergent result of the model concerns the parameter value of knowledge *K*. As knowledge becomes more valuable in terms of extra life-span, the equilibrium proportion of *L*-types increases and the equilibrium proportion of *TL*-types decreases (cf. Figure 10). This counterintuitive result can be explained as with their prolonged lifetime fewer *TL*-types and thus a lower amount of knowledge are sufficient to establish a successful exploitation regime. An increased value of knowledge keeps fewer altruists alive.

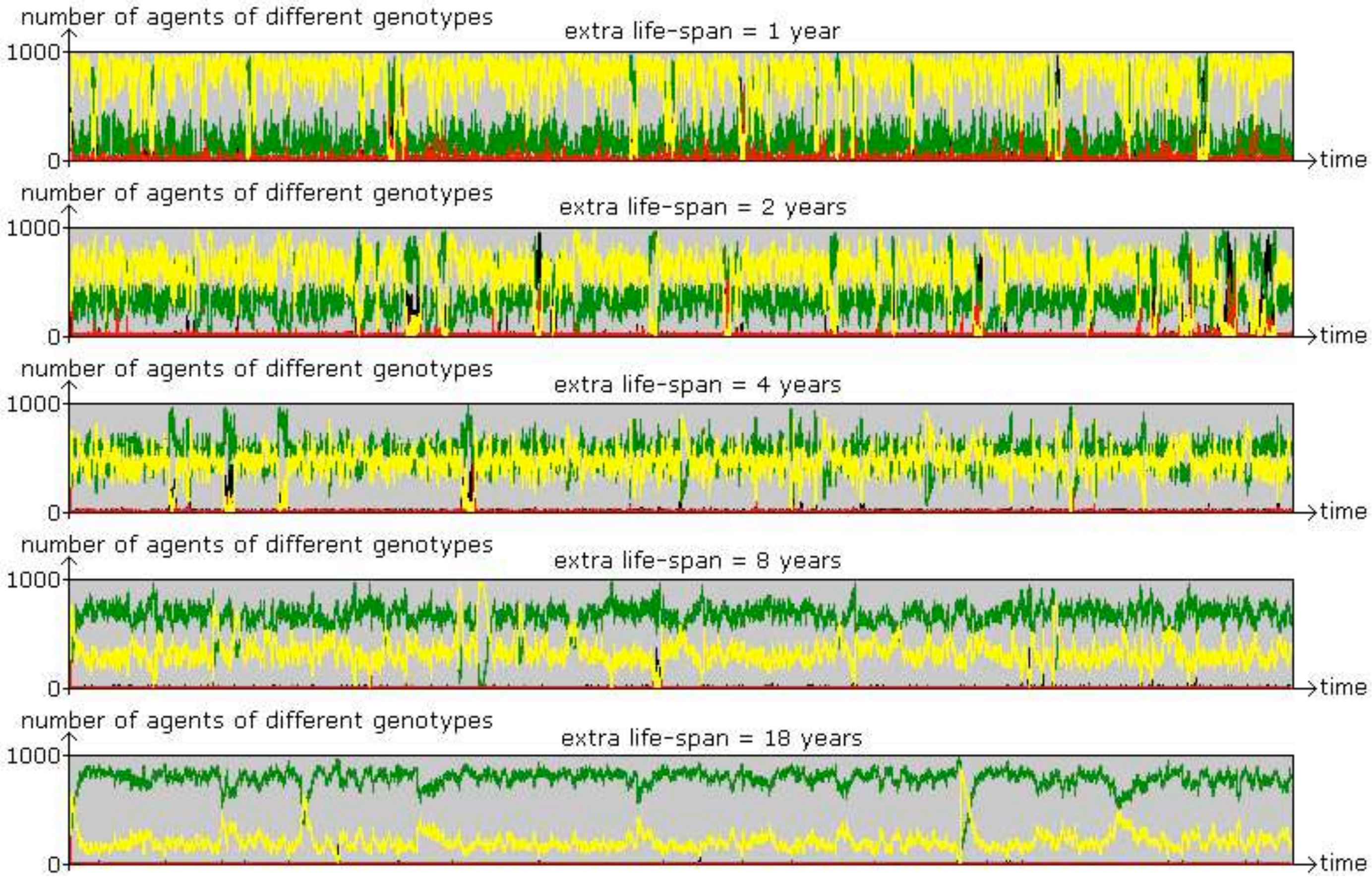

Figure 10. The Paradox of Knowledge
By increasing the value of knowledge in terms of extra life-span, the proportion of greens (*L*) increases in the mixed equilibrium.
Parameter values are the same as before with the population size of 1000.

Some illustrative robustness tests

4.13

We have performed several additional analyses to see whether our main conclusions hold also for different combinations of auxiliary parameter values. Increasing the *mutation rate* brings in more stochastic fluctuation and destabilizes patterns of stable regimes in small populations. With an increase in the mutation rate from 0.1% to 1% the typical population becomes mixed, but the success of altruistic *TL*-types is even more apparent. Starting from a random population of 100 agents, *TL*-types gain full dominance first in 66% of the cases compared to 34% of the cases with a mutation rate of 0.1% (based on 1000 runs each, proximity based interaction, other parameters are fixed as before). For large populations, however, an increased mutation rate is somewhat disadvantageous for *TL*-types (Figure 11).

Figure 11. Illustrative tests of robustness
Proximity based interaction, starting from a random mix of agents (year 0) with a population size of 1000. The lower part shows results for the reference parameter values. In the middle, the mutation rate is changed from 0.1% to 1%. In the upper part, lifetimes of agents are doubled.
All other parameter values are fixed as before.

4.14

It is not much of a surprise that with an increase in *innovation rate*, the success of altruistic *TL*-types is even more evident. The early appearance of knowledge provides a better soil for the early dominance of *TL*-types. With an innovation rate of 1% they gain full dominance first in 61% of the cases compared to the reference result of 34% (based on 1000 runs each, other parameters are fixed as before in proximity based interaction with 100 agents). We observe self-explanatory effects also when varying the *breeding range* parameter. A close range means that benefits of teaching go more likely to agents of the same genotype, hence there is a higher success of *TL*-types (0.39, 0.34, 0.27 probabilities of first full dominance for breeding ranges of 10, 20, 40 pixels, ceteris paribus).

4.15

There is some non-linearity in the effect of the *basic life-span* parameter that can be explained similarly as the paradox of knowledge. Doubling the length of lives results in 58% chance for *TL*-types to gain full dominance first in a population of 100 agents, which is clearly higher than the reference level of 34% (longer life means more opportunities for innovation). On the other hand, being the first to gain dominance in a small population does not mean higher success in large populations. As Figure 11 shows, when all agents live longer, the proportional distributions are shifted in favor of the free rider *L*-types. This is because the longer lifetime of *TL*-types provide better opportunities for exploitation.

Discussion

5.1

This paper presented the results of an agent-based simulation to demonstrate how pure altruistic teaching that is neither reciprocal nor dependent on kin recognition could evolve. Teaching was modeled as a dyadic interaction in which one agent provides knowledge for the other, bears the costs of this action, and receives nothing in exchange. It was not necessary to assume that agents have any kind of cognitive capacity about past interactions nor that they can distinguish between their partners, hence results could also be applied to non-human populations.

5.2

The study confirmed previous results that a learning capacity is a successful trait selected by evolution, but only if there is something to learn. More importantly, our results demonstrated that altruistic teaching gains an overwhelming evolutionary success in a spatially structured population where individuals encounter each other on a proximity basis, if it is combined with the capacity to learn. Although altruism in this context was specified as sharing knowledge with others at a certain cost, the results illustrate how "pure" altruism that is neither reciprocal nor directed merely towards kin could evolve.

5.3

The success of altruism is due to local reproduction and interaction where altruists are likely to meet others with the same genes. Although we conceptualized benefits of altruism in terms of survival chances and the costs of altruism in terms of reproduction chances, one might interpret our results in the context of the theory of kin selection (Hamilton 1964a; 1964b). From this theory it follows that the frequency of the teaching gene in the population only increases if the benefits of teaching fall sufficiently often to other carriers of the gene. More specifically, evolution favors altruism if $rK - C > 0$, where r is the degree to which benefits accrue to other altruists compared with average population members (Doebeli and Hauert 2005). In viscous populations, limited dispersal promotes interactions among relatives (Hamilton 1964a; Grafen 1985). In opposition to random matching, in case of a spatially structured population this is what happens.

5.4

The evolution of "pure" altruism, however, is not due to kinship based altruism that can be attributed to "selfish genes" (Dawkins 1976). The important distinction is that in our model, agents do not adjust their behavior towards their kin, nor select their interaction partners based on kinship; they simply help those who are in their proximity. Kinship based altruism in the theory of selfish genes requires the recognition of kin, which is a debatable presumption in many cases. Furthermore, it is also unable to explain altruism towards adopted children or encountered strangers. Our results, on the other hand, do not imply that proximity based altruism would be in any way more successful than kinship based or reciprocal altruism when differentiation can be made or indicators of relatedness can coelvolve (cf.Axelrod, Hammond, and Grafen 2004).

5.5

The agent-based simulation presented in this study highlighted important emergent consequences of the evolution of altruism. The success of altruistic teaching has led to the settlement of agents. The population stopped moving around and settled around centers of knowledge. This result suggests a new possible perspective that group formation and settlement could have evolved as a consequence of the spread of altruism.

5.6

Another important result is that increasing the benefits of altruistic teaching in large populations lead to a lower percentage of altruists in the population. This contradicts predictions based on the theory of kin selection, in which inclusive fitness and frequency of altruists in the population increases with the benefits provided by helpers to others (cf.Hamilton 1964a).

5.7

This study discussed the evolution of proximity based altruism in spatially structured populations, but proximity can also be interpreted in a wider societal context, as social distance. An extension of this study could highlight the success of altruism in different social network structures, such as small world networks. Another extension could examine the evolution of proximity based altruism and the resulting emergent phenomena in different social dilemmas.

Appendix: Pseudo-code for interaction in one year (round) of the simulation

```
for (every living_agent x):
        if (random(1000) < innovation_rate) x.knowledge:=1;
        if ((x.teacher) && (x.knowledge=1)):
                repeat // search for an agent without knowledge
                        if (proximity_based) y := random_agent_in_proximity
                        else y := random_agent;
                until (y.knowledge = 0)
                if (y.learning) y.knowledge := 1;
                x.breeading_chance := x.breeading_chance - costs;
        end if
end for
```

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Notes

[1] The simulation was written in Delphi and can be downloaded from http://www.uni-corvinus.hu/~tkaroly.

[2] For parameter values as in Figure 3, without knowledge at the start and with random matching, the total length of regimes of the *TL*, *L*, and *0* genotypes are approximately the same.

[3] The analysis has been replicated by omitting variation on the *L*-gene, thus “switching off” genotypes *T* and *0.* In small populations, *L*-types are relatively more successful with switching off than without switching off variation in the learning gene, but their chances to attain dominance lags behind the chances of *TL*-types in a spatially structured population. Results about the evolution of altruistic teaching in large populations do not differ from the

presented results when genotypes *T* and *0* are excluded.

[4] For the assumed parameter values in a small population, regimes of the *TL*-types last four times longer than regimes of the *L* or *0* genotypes and more than six times longer than *T*-regimes. Results confirm that learning from others (expressed by the *L*-gene) is successful, but the gain from the capacity of learning is negligible if there is no knowledge around.

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